DOCUMENT RESUME

ED 262 054 TM 850 529

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TITLE The Evolution of Learning Mechanisms.
PUB DATE Aug 84
NOTE 68p.; Paper presented at the Annual Meeting of the American Psychological Association (92nd, Toronto, Ontario, August 24-28,1984).
PUB TYPE Speeches/Conference Papers (150) -- Information Analyses (070)

EDRS PRICE MF01/PC03 Plus Postage.
DESCRIPTORS Animal Behavior; *Behavioral Science Research; Behavior Development; *Biological Influences; Conditioning; *Evolution; *Learning Processes; *Learning Theories; Literature Reviews; Psychology; Researchers; Scientific Methodology
IDENTIFIERS Behaviorism

ABSTRACT

This paper introduces seven principles of learning, enduring over the last five centuries of psychological thought, to discuss the evolution of the "Biophyche" (the brain in action) in the development of humans and other large organisms. It describes the conditioning theories of Darwin, Pavlov, and Thorndike and critically reviews the twentieth century behaviorism (Watson, Spence, and Skinner) which separated the psychology of learning from biology. The selective pressure of the food chain on the evolution of corporal structure, instinctive behavior, and learning mechanisms is discussed in terms of body and brain, prey and predator, the memory for poison, the memory for pain, the bicameral biophyche, and sensory hedonistics. Both behavioral and physiological solutions have been used for problems of survival. Imprinting is used to illustrate the subtle interplay between instinct and learning. Uses of the geomagnetic field for navigation by humans, birds, and bees illustrates a convergent evolutionary force. While the evolutionary origin of learning is problematical, learning is always an adjustment of a natural behavioral pattern inherent in the anatonomical structure. In conclusion, learning is the primary instinct because it converts a potentially hostile environment into a comfortable territorial home where secondary instinctual processes can take place in safety. (BS)

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THE EVOLUTION OF LEARNING MECHANISMS

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Master Lecture
American Psychological Association
1984 Annual Meeting, Toronto, Canada

TM 850 529

SEVEN HISTORIC PRINCIPLES OF LEARNING

History is selectively recalled at each point in time according to the current purpose of the author. Our purpose is to introduce seven scientific principles of learning which have endured over the last five centuries of psychological thought and study. Seven is the favored integer when professors are enummerating universal laws, basic ethics or personal homilies. George A. Miller (1956) discusses this human proclivity in a delightful paper entitled: The Magical Number Seven, Plus or Minus Two: Some Limits on Our Capacity for Processing Information. We tend to distinguish seven shades of gray and feel seven degrees of wonder. That integer nicely describes our span of apprehension and comfortably fills our capacity for short-term memory. Call it the "psychobiological number seven" because that capacity must be the endpoint of a long evolutionary process of adaptation to this earth. It may not be the perfect capacity because evolution does not strive for perfection; evolution is a "blind" process resulting from differential reproductive success due to biological variations among organisms.

First, let us recommend an excellent source for those who enjoy reading the historic literature of our field. William S. Sahakian (1981) has skillfully compiled and edited the writings of many philosophers and psychologists creating a single coherent volume entitled History of Psychology. These exerpts give the reader an insight into many important figures beginning with ancient Greek and Latin Philosophers, coursing through medival scholars and renaissance dissidents and culminating in writings of the evolutionists, the experimentalists and the behaviorists. The book provides an exciting preview and a useful guide to the history of psychological thought.

The beginnings of modern learning theories can be traced to the writers of the European Renaissance who rejected medieval notions of a soul oriented towards the deduction of heavenly wisdom and proposed in its stead, an inductive associationistic mind focused on earthly observations. In doing so, they set up the basic principles of learning which exist to this day. These writers were not giants nor are we dwarfs, but as Juan Luis Vives said, we are both human and we become taller visionaries by adding their stature to our own, providing we do not throw away our advantage by prostrating ourselves these famed authorities. Vives advised his students and colleagues to cease their disputations on antiguities and to study nature (Watson, 1915).

Given our Spanish surname, one might question our objectivity in recalling Juan Luis Vives, a Catholic Philosopher and Educator born in Valencia in 1492. However it was a Welsh scholar, Foster Watson (1915), who called Vives "The Father of Modern Psychology". Furthermore, Sahakian records his birth in 1492 as a "landmark in Psychology" identifying him as the author of De Anima et Vita and precursor of "modern psychology". Zilborg (1941) described him as the humanitarian advocate of the first psychiatric revolution against demonology. He cites Vives' empirical advice for treatment of the insane as follows: "Remedies suited to the individual patients should be used. Some need medical care and attention to their mode of life; others need gentle and friendly treatment, so that like wild animals they may gradually grow gentle; still others need instructions." This statement, which so resembles the "watching, wondering and taming procedures" suggested for treating autistic children by Nikolass Tinbergen (1974) in his Nobel Laureate address, was written about three centuries before Philippe Pinel began the final psychiatric revolution by removing chains and providing medical

treatment for demented human beings in France.

Vives is well-known in Europe and Latin America, but he is an obscure figure in American Psychology because of political and religious persecution. He was a member of the English Court and a Lecturer at Oxford, but he was also Spanish and Catholic, so he fell from favor during the divorce of Catherine of Aragon and Henry VIII and the schism between the Tudors and the Catholic Popes. His humanistic writings were largely expurgated from English Letters during the subsequent rivalry between Elizabeth I of England and Phillip II of Spain. Ironically, his father was persecuted in Spain for being a Jew, and Vives, who escaped from England to Flanders, never returned to his beloved Valencia (Watson, 1915; 1922). Vives deserves a prominent place in the history of science for several reasons. First, he taught <u>empiricism</u> at Oxford, two generations before Frances Bacon, moreover, Vives self-consciously applied empiricism to human psychological problems in a way that Bacon did not do. Thus, Vives provides us with the first principle of science:

I. <u>Empirical analysis begins with the observations of nature and proceeds to explanation by inductive logic, then returns to nature for verification.</u>

Empiricism was a radical transition from the prevailing medieval viewpoint. For example, Saint Augustine discussing the soul-like nature of mind excluded from consideration all outside knowledge received through the senses of the body, and began with the dictum that all minds know and are certain of themselves (see Sahakian, 1981, p. 16). In contrast, Juan Luis Vives wrote, "The senses are our first teachers in whose home our mind is enclosed". Vives was not concerned with essence of the soul, only with the practical manifestations of soul in mind and action. Furthermore, knowledge

was of no value to Vives until it was applied to social problems (Watson, 1915).

Second, Vives analyzed the behavior of animals and other people, as well as his own introspective memories and feelings. In his age, equating souless animals with godlike humans was a courageous stand for a Church scholar. Nevertheless, he noted that if an animal is called and then treated with something pleasant, subsequently it will run towards the caller readily. But if the animal is called and beaten, it will be frightened by the memory of the beating when it is called again. The same is true of people, when something joyful occurs in a certain place and time, pleasant memories of that place are formed, but if a sad event happens then the memories of that place are sad. Vives recalled his own memories as a child eating cherries in Valencia while ill with a fever. "For many years afterwards," he said, "whenever I tasted fruit, I not only recalled the fever but also seemed to experience it again" (Watson, 1915). This broad spectrum of evidence extending from behavior of other living forms to self-reports implies:

II. <u>There is a continuity of mind and behavior among living organism so that information obtained in observing one organism can be generalized to other organisms.</u>

Third, Vives formulated associationism two centuries before John Locke. According to this theory of mental chemistry which underlies all modern psychology, the mind is a recording system which stores and integrates mental elements. These discrete sensations, motives and reactions emmanating from the body are formed into compounds called ideas by the action three basic laws of association as follows:

III. <u>Mental elements are associated (1) by their contiguity in time and</u>

space. (2) by their similarity to each other. (3) by their cause and effect relational sequences.

For Vives, as for most modern theorists, contiguity was the most important associative law. When two things have been perceived together, the appearance of one recalls the other to mind, he said. On recalling a place, one recalls the people encountered there, and the fears, emotions and motives felt in the place. Thus the various elements are welded together in conscious stream of memory and thought (Watson, 1915).

Association by similarity hardly needs elaboration; it is represented in modern psychology by discrimination and generalization learning. Association by cause and effect can be viewed in two ways. It can be viewed physicalistically, as it was by Hume (1739/1969) who argued that it could not be distinguished from contiguity. But Hume rejected feelings from his analysis; psychologically, cause and effect comes from feelings of causality. The association expressed by Luis Vives, when he said each time he tasted cherries he seemed to feel the fever again, is an example of the cause and effect, now known as the "law of effect".

Juan Vives suffered obscurity in modern textbooks, but John Locke suffered a worse fate, distortion and defamation. He is often depicted as the author of the ridiculous behavioristic idea known as the tabula rasa, the implication that the mind of a newborn babe is a blank slate which passively records external inputs. In truth, Locke was a brilliant physician with an astonishingly modern view of sensory integration and reflexive action. In our judgment, he is the outstanding physiological psychologist of his age or any other age. It is a humbling experience to read his Essay Concerning Human Understanding (1690/1981) written exactly three centuries ago; we have made so

little progress since then (see Sahakian, 1981, pp. 32-34). Locke delineated two sources of knowledge:

IV. Through experience, the sensations induced by external objects and events are transmitted by the nerves to the sensorium, then the innate connections and operations of the body give rise to the reflections of the mind.

Sensation and reflection foreshadowed stimulus and response as well as releasing sign and species-specific reaction. Locke knew the mind and the body were inseparable. Over a century before Johannes Muller (1838/1981) proclaimed the "doctrine of specific energies of nerves" Locke defined the doctrine and provided examples. He said, in effect:

V. Sensations do not exist in external events and objects, sensations are the effects produced in our receptors, nerves and brains by external events. The "external" world is constructed for each organism by the organism itself.

In discussing manna, a dried exudate of plants used as a medicinal purge, Locke (1690/1981) explained that the sensations of whiteness, sweetness and illness did not exist in manna, but were the effects produced by manna on eye, palate, and gut, respectively. In the following analysis employing the notion of kinetic energy as heat, he explained how a cool left hand and a warm right hand plunged into the same basin of tepid water sense warmth and coolness respectively at the same time. Obviously, the water cannot be both cool and warm, hence the opposing sensations of heat and cold must be due to changes in the motion of the tiny particles in the nerves, increasing in the left hand and decreasing in the right hand, caused by the intermediate motion of tiny particles in the water.

This great idea has broad implications for the comparative study of those organisms which have receptors and nerves different than our own. Locke (1690/1981) warned that in this vast universe there are many mansions occupied by different organisms, of whose mental faculties we have as little knowledge "as a worm shut up in one drawer of a cabinet, hath of the senses or the understanding of a Man." Therefore, generalization from one organism to another must be preceeded by a comparative analysis of their sensory systems and their brains.

John Locke scrubbed the theoretical mind clean of the accumulation of two millennia of Platonic rationalizations but he enriched it with biological structure and function. He was a political rebel disputing the heavenly knowledge dispensed by the religious hierarchy. He favored the civil rights of individuals over the divine rights of Kings. To the questions: What distinguishes the mind of the King from that of the commoner? Locke replied "experience". How could a commoner acquire the knowledge to rule? Locke replied "by observing". This thesis is presented in a most entertaining form by George Bernard Shaw in Pygmalian and in the musical comedy version of this play, My Fair Lady, where a linguist turns a flower-girl into a "princess" by an education in aristocratic speech and manner, the behavioral manifestations of a royal mind.

The reply to John Locke's theory of mind came in 1781 from Immanual Kant, (1896) who conceded everything to empiricism except a few a priori intuitions, which he argued, must exist in the mind prior to any experience (see Sahakian, 1981, pp. 69-72). Therefore, Kant is recalled for two of his intuitive propositions which set the context for recording all phenomena in mind and memory:

VI. An a priori appreciation of space is a necessary representation in mind which precedes perception of external objects.

Kant argued that while it is possible to imagine space without objects, it is impossible to imagine objects without space. Therefore, space is not determined by objects, but rather a sense of space is a necessary contextual condition for the perception of objects (see Sahakian, 1981, p. 69). It is true that most organisms studied seem to be able to remember spatial arrangements of objects as if they acquire a "cognitive map" of their territory. Kant made a similar argument for a sense of time:

VII. An a priori appreciation of time is a necessary representation of mind which preceeds perception of external events.

Kant said that while it is possible to imagine time without events, it is impossible to imagine events without time. Therefore, time is not determined by a sequence of events, but rather, a sense of time is a necessary contextual condition for the perception of events (see Sahakian, 1981, p. 71). It is also true that most animals seem to have cyclical functions which operate like biological clocks. Whether space exists prior to exploration, and whether biological clocks runs free of external events, is open to question. However, it seems certain that a mature mind cannot function adequately without a sense of space and time with which to categorize objects and events, however that sense may come into being.

SEVEN PRINCIPLES APPLIED TO THE BIOPSYCHE

Undergraduate students refer to the dual major of Biology and Psychology as "biopsych" thus the modern concept of mind could aptly be called the "biopsyche". Despite the protestations of the "behaviorists", we doubt if anyone is really interested in behavior per se, everyone is interested in

behavioral indicators of those central states of motivation and memory which give rise to the characteristic habitual patterns of an individual or of a species. The central nervous system, principally the brain, is the structure of the biopsyche in creatures of our sort. The functional biopsyche is the brain in action. Brain structure and function represent a single inseparable product of evolution.

Evolution is a divergent process driven by variation of structure and function. Theoretically, all forms of life emerged from a single form due to biological variation. The varying individuals fanned out upon this earth to find ecological niches best suited to their idiosyncracies of structure and function in a process called "adaptive radiation". The ecological niche is an important, yet circular, concept because the niche cannot be described without recourse to the organism filling it. No biologist would have ever conceived of an ecological niche composed of low winter territory in India and a high summer territory in Tibet joined by a long narrow flight path arching above the world's highest mountains, yet this is the "niche" created by the bar-head goose. Conversely, the special structures and functions of any organism cannot be understood without recourse to the ecological niche in which the the organism evolved. To traverse the distant regions of its niche, the bar-head goose has acquired the brain capacity to navigate over "the hump" of the world and the cardiopulmonary capacity to fly at 30,000 feet, honking at every beat of its wings. Flying in the pressurized cabin of a jet plane, we often wonder how a warm-bodied creature, such as the bar-head goose, can even survive in what is a thin cold "hostile" environment to us. But, the organism and its niche are two aspects of the same phenomenon and the bar-head goose must be "comfortable" out there. As we change "our" environment, we change niches and

so, inevitably, we lose organisms and species.

The Nature of Science.

Principle I refers to the general process of accumulating scientific knowledge via empirical observation and arriving at tentative explanations through inductive logic. This dynamic method is also part of nature. As Lorenz (1965) points out, the acquisition of specialized anatomical structure through evolution, and the acquisition of individual knowledge through experience, are similar empirical inductive processes: (A) By death and survival, a species acquires the specialized structure enabling it to survive in its niche. Therefore adaptive structure represents eons of ecological information accumulated by natural selection and encoded into the genome for transmission to succeeding generations. (B) By failure and success, each individual acquires information about the vagaries of its particular niche and encodes it into memory for use when similar situations arise again.

Behavior is manifested at the juncture between the organism and its niche and learning is an adjustive process which eases the misfits between the two. All organisms inherently possess the basic behavioral patterns which enable them to survive in their niche, but learning provides the fine tuning necessary for successful adaptation. Even fetal organisms must learn. For example, if a rat fetus is presented with lemon-flavor while it is in the uterus, it will show a higher preference for lemon-flavored nipples on its mother after it is born. If the flavor presented to the fetus is followed by a mild toxicosis in utero, the newborn rat will display a reduced preference for a nipple marked with that flavor (Pedersen, Williams, & Blass, 1982; Smotherman, 1982; Stickrod, Kimble, & Smotherman, 1982; Kolata, 1984).

Newborn human infants demonstrate inherent wisdom concerning food and

flavor. Tickle a baby's cheek with a cotton swab and it will turn its head and engulf the swab in its mouth though it has never eaten before. If the swab is bitter, the baby grimaces and thrusts out its tongue as if it knows that bitter is the natural signal for poison. If the swab is sweet, it will suck with a benign expression as if it knows that sweet signifies nutritious calories (see Garcia et al., 1982; and Garcia & Hankins, 1975). These inherent human preferences can be modified in utero as the rat data indicates. This conjecture is almost certainly true since infants of both species have the required homologous brain structures, and the rat is the lesser developed of the two at birth.

In the first few days of life, the human infant demonstrates a preference for its mother's voice over another woman's voice. It prefers its mother's heartbeat over its father's voice. The infant also prefers to listen to a poem which it heard in the womb, as its mother read it, to another poem with a different meter when both poems are read by its mother. The babies select what they want to hear by sucking in different patterns on a nonnutritive rubber nipple (DeCasper & Fifer, 1980; Kolata, 1984). Certainly the newest member of our family was far from helpless at birth. She immediately created her niche eliciting a maternal embrace and attaching herself to her mother's breast. At seven months, she has developed vocalizations and expressive movements to enthrall her parents and grandparents and smiles to reward them for assisting her to achieve her ends. For example, establishing eye-contact with her grandfather, she made authoritative sounds from the back of her throat, before picking the forbidden eyeglasses out of his shirt pocket. Then forestalling him with another stern "declaration", she began chewing on the ear-bars. So meaningful were her intonations and so exquisite was her timing

that, without uttering a single word, she effectively argued her rights to expropriate his glasses.

Nature and Nurture.

When discussing a child's development, the nature-nurture argument inevitably arises, usually phrased in the following form: Which is more important, heredity or environment? Attempts to answer the question employ simple statistical formulations, such as $V_H^2 + V_E^2 = 1$, which means that the variance in a trait can be divided into a heredity component (V_H^2) and an environmental component (V_E^2). Ponder this equation for a moment. If V_E^2 decreases, then V_H^2 must increase, and vice versa. Furthermore, either component can be reduced to zero. These statistical functions make no biological sense. Of course, it is said that these are merely simplifying assumptions dealing with the relative variance in measured traits of groups. It is also said, the reasonableness of the assumptions vary with the particular case in which they are applied, and the resulting proportions obtained from groups cannot be meaningfully applied to any individual. Nevertheless, the pronouncements issued following these statistical studies usually sound like general laws with definite implications for social policy. Indubiably, there are genetic differences between groups of people but since we cannot predict the future with much precision, we cannot tell which genetic variants, if any, will prove more adaptive in the long run.

Hereditary and environmental influences are so completely intermingled that it is impossible to what degree either influence is responsible for any structure or trait displayed by an organism. As we pointed out above, the genome itself can be considered an accumulation of hereditary-environmental interactions. Furthermore, beginning with the zygote and continuing at every

step of its development, the living organism is the result of a series of interactions as the genetic code is expressed on an environmental substrate by biochemical reactions, much as an image is developed on a photographic plate. Change the light striking the same emulsion and the picture changes; change the emulsion receiving the same light and the picture changes. Which is more important pictorially, light or emulsion?

Arguments on "nature or nurture" remind us of how Pudd'nhead Wilson got his name (Mark Twain, 1893). Listening to a dog yelping, snarling, howling and making a disagreeable nuisance of itself, Wilson said:

"I wish I owned half of that dog."

"Why?" somebody asked.

"Because I would kill my half."

The group that heard Wilson's comments retired to discuss him in privacy. Obviously it did not matter biologically, if Wilson meant to kill his end of the dog as opposed to the other persons end, or if he meant he would kill his half-interest in the general dog. However, in the latter case, it would be more difficult to determine legally whose half he had killed. Finally the puzzled group deemed him a fool and thereafter called him "Pudd'nhead".

Pervasive Ecological Influences.

Large organisms resemble each other, in part, because they all share a common ancestor and, in part, because they have been shaped by the same general environmental forces such as oxygen, temperature and gravity. By "large" we mean minnows, shrews and humming birds, as well as sharks, elephants and ostriches. Most insects are also large. Minute organisms occupying mansions where surface tension and fluid viscosity are greater impediments to movement than gravity are excluded from this discussion

although the remote ancestor of all large organisms must have been a tiny cell living in such a world. They are simply excluded, because as Locke said, we have little knowledge about the universe in which they cope.

Five of the seven principles of learning can also be considered pervasive ecological influences on all large organisms. For the moment, we will exclude Principle IV (senses and reflexes) and Principle V (neural transduction) which deal with the internal structures common to all large organisms. We have already made the case for the persuasive influence of Principle I (empiricism) when we discussed the inductive logic of natural selection and of individual experience. We also made the case for Principle II (continuity of life) when we discussed fetal learning in rat and child. It is intuitively obvious that all organisms must cope with Principle VI (space) and Principle VII (time).

Let us now consider the persuasive influences of Principle III (associationism). If two objects are close together in space, or if two noises are heard in quick succession, it is probably safer to assume they are connected rather than separated, thus association by contiguity has a degree of ecological validity for all large organisms. If two objects look or feel the same, it is probably safer to treat them the same, therefore association by similarity is an adaptive process acquired by all organisms through natural selection. If a stimulus such as taste is followed by a sensation such as illness, it is adaptive to consider them cause and effect. The same can be said for a noise followed immediately by a painful insult to the skin; it is adaptive to run or hide when that noise is heard again.

Associative learning and acquired habits played a critical role in Darwinian theory from its inception as illustrated in Figure 1. Darwin's (1871/1936) volume on the origin of species contains numerous examples on the

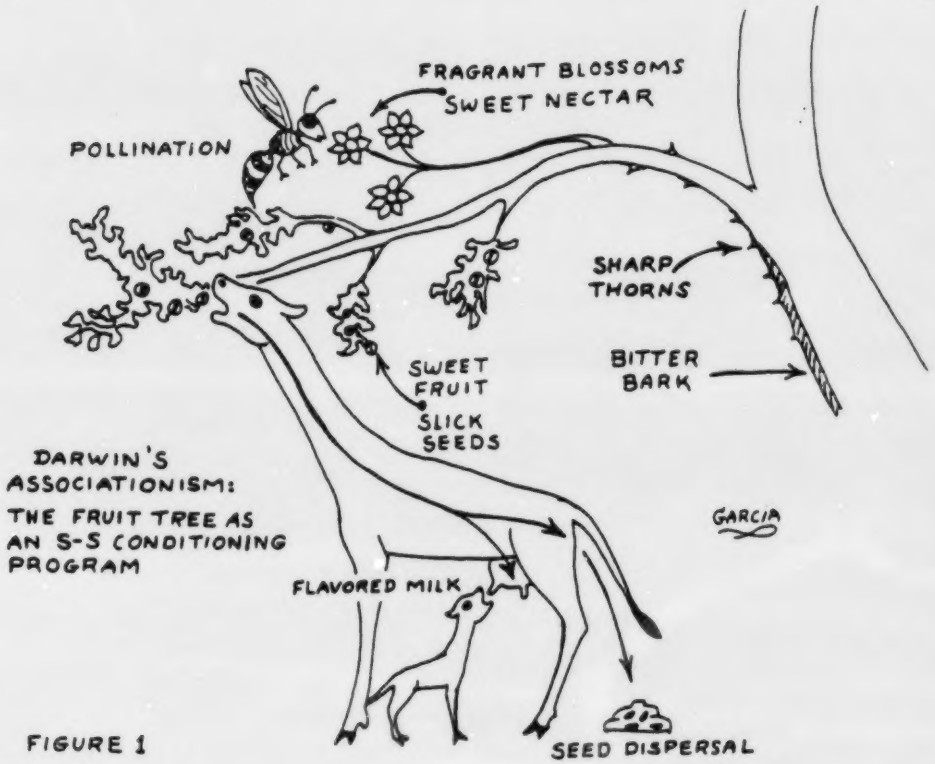

FIGURE 1

Figure 1 illustrates the associationistic assumptions implicit in Darwinian theory. The fruit tree has sharp thorns and bitter bark to protect its vital structures from browsers. With fragrant blossoms, it signals bees that sweet nectar is available--and the bee carries its pollen to a similar blossom in another tree of the same species. Fruit is a combination of nutritious pulp and slick digestable seeds--the animal digests the pulp and drops the seed in far-off places. The tree benefits because animals learn. Mammals acquire preferences for certain foods, food flavors the milk, thus the offspring acquires a preference for the same food as the mother. In the case of the giraffe, an acquired preference for the leaves of tall trees may have set the stage for natural selection of long necks.

coevolution of plants and animals. The common example is the blossom and the honey bee. The bee goes from flower to flower collecting nectar and delivering fertile pollen as it does so. This process becomes marvelously complex as the plants evolve special visual signals to beckon certain bees and special mechanisms such as a lock on the "nectar cabinet" which can be tripped effectively by heavy bumblebees. This encourages the bumblebees to specialize on specific blossoms, thus making them efficient pollinators of a particular plant species. Since Darwin's time we have learned that bees are tiny learning machines capable of associating arbitrary signals with food under artificial experimental conditions. For general references on the coevolution of animals and plants, see Alcock (1979) and Gilbert and Raven (1980).

Lamarck, Darwin and the Giraffe's Neck.

Learning may be a causal factor in evolution. We mean that the capacity to associate sequences and patterns of events in time and space, and to retain this information, may have given rise to the differentiation of modern animals from common primal ancestors. This is an old idea considered a heresy in modern biology, attributed to Jean Baptiste de Lamarck, who published a theory of evolution in 1801. Lamarck believed that differentiation of animal forms arose out of the use or disuse of organs during adaptation to the environment. Through habitual exercise, some organs were developed, some were neglected and these acquired characteristics were passed on to the next generation. He described the giraffe's neck as an example of the effects of habitual use upon specific structure.

Fifty years later, Charles Darwin (1871/1936) used the same example of Lamarckian evolution in the Origin of Species: For some unknown reason, the primal ancestor of the modern giraffe began browsing on the leaves of tall

trees. In hard times when leaves were scarce the individuals stretching their necks the longest survived and passed this acquired characteristic to their progeny. "By this process" wrote Darwin, "...combined no doubt in a most important manner with the inherited effects of the increased use of parts, it seems to me almost certain that an ordinary hoofed quadruped might be converted into a giraffe." Now Darwin is credited for establishing Darwinian evolution and Lamarck is discredited for proposing Lamarckian evolution, which proves that science as well as mythology needs its heroes and its heretics clearly delineated.

Darwin was not wrong in cribbing from Lamarck, he simply lacked detailed knowledge of the way in which characteristics were transmitted from one generation to another, though he made some shrewd guesses foreshadowing two types of inheritance mechanisms. Ironically, at the very time he was engrossed in this problem of transmission, Gregor Johann Mendel (1865/1959) was establishing the principles of genetic transmission working with flowering sweet peas in a monastery garden in Monrovia. Ultimately this new science indicated that the habits of animals had no dirct effect upon their genes. In the case of the giraffe, the genetic changes which resulted in long and short necks were "random", like the toss of dice, and the "lucky" ones who got the long necks survived and passed their genes on to their offspring. Thus environmental pressure, operating blindly and mechanistically through gene selection, encoded information about a way of life into the anatomical structure of the giraffe.

However, genetic mechanisms are not the only mode of transmission from parents to offspring. Learning is another mode as Lamarck and Darwin foresaw. Consider again the ancient quadruped munching on the leaves of tall trees. We

now know that during consumption, sensors on the tongue send taste information and sensors lower down in the gut send nutritional information to the brain. Midbrain mechanisms increase the palatability of nutrients from tall trees so that the animal acquires that peculiar habit of dining. The diet of the mother flavors her milk so that acquired preference is transmitted to her young and thus the stage is set for the competition wherein the length of the neck is a crucial factor (see Figure 1).

As we discussed before, natural selection and associative learning operate together. Bitter is the natural signal for poison and any animal insensitive to bitter is at risk. This risk is reduced if the animal nibbles at new foods and is able to associate the bitter flavor with mild toxicosis. Sweet is the natural signal for highly caloric nutrients and animal insensitive to sweet is also at a disadvantage, but it also can compensate for this deficiency by an associative learning mechanisms. A wide variety of animals, including neonate rats and humans, have both the inherent predispositions toward food selection and associative food-effect mechanisms.

THREE MODERN CONDITIONING THEORIES

As the 19th Century turned into the 20th Century, three modern conditioning theories were put forth by Darwin, Pavlov and Thorndike, respectively. All three systems were based upon the Seven Principles in general, and on Associationism in particular. They were modern theories, which is to say: Stimuli replaced sensations and responses replaced reflections as the words denoting the psychological elements. Habits replaced ideas as psychological compounds. Introspection was replaced by theorizing, and hypothesis-testing and arguments were resolved by experimentation and data collection.

Darwin, Pavlov and Thorndike did not compete with each other by offering alternative explanations for the same set of facts. Each system dealt with a different data base and was compatable with the other two. All three systems focused on feeding behavior and invoked biological adaptation and associations in their explanations. To view them as phases of the same psychological process, one must rearrange history: Thorndike was explaining how the organism coped with the problem of obtaining food. The Thorndikian, or instrumental phase, began with food beyond a barrier of time and space and ended when food was accessible to the animal. Pavlov was explaining how food was utilized. The Pavlovian, or consummatory phase, began when food-related stimuli elicited anticipatory oral responses and ended with food ingestion. Darwin was interested in the ultimate effects of the food chain. The Darwinian, or the ultimate adaptive phase, began with prey coloration and predator reactions and ended with natural selection.

Darwin and the Gaudy Caterpillar.

In a previous paper, Garcia et al. (1975) described a hypothetical-deductive Darwinian Learning model that antidated the Classical Conditioning and Instrumental Conditioning theories by nearly a half century. Darwin was discussing an exception to adaptive value of camouflage. Cryptic form and coloration is a popular defense against predators in the natural world, as it is against the enemy in human warfare. Yet some caterpillars flaunted their brilliant colors on the tips of the bare twigs catching the eye of every passing bird. These facts placed a severe burden on Darwin's theory of adaptation through natural selection. He presented his dilemma to the other evolutionist, A.R. Wallace, and then recorded the following hypothesis in his Descent of Man (1896).

> From such considerations Mr. Wallace thought it probable that conspicuously-coloured caterpillars were protected by having a nauseous taste; but as their skin is extremely tender, and as their intestines readily protrude from a wound, a slight peck from the beak of a bird would be as fatal to them as if they had been devoured. Hence, as Mr. Wallace remarks, 'distastefulness alone would be insufficient to protect a caterpillar unless some outward sign indicated to its would-be destroyer that its prey was a disgusting morsel.' Under these circumstances it would be highly advantageous to a caterpillar to be instantaneously and certainly recognized as unpalatable by all birds and other animals. Thus the most gaudy colours would be serviceable, and might have been gained by variation and the survival of the most easily-recognized individuals.

Wallace presented his hypothesis to the Entomological Society of London in 1866. Twenty years later E.B. Poulton (1887) reviewed the evidence substantiating a theory of conditioned taste aversions in a remarkable paper of 83 pages entitled, The Experimental Proof of the Protective Value of Color and Markings in Insects in Reference to their Vertebrate Enemies. He described how food becomes aversive when it is followed by toxicosis and how the visual aspects of food are avoided when followed by nauseous taste in a chain of behavioral reactions. A few unpleasant experiences are sufficient to establish a prejudice against an insect and against any eatable species which resembled the noxious one.

Darwin (1896) summarized his own conclusion as follows:

> When the birds rejected a caterpillar, they plainly shewed, by shaking their heads, and cleansing their beaks, that they were disgusted by the taste. Three conspicuous kinds of caterpillars and moths were also given to some lizards and frogs, by Mr. A Butler, and were rejected, though other kinds were eagerly eaten. Thus, the probability of Mr. Wallace's view is confirmed, namely, that certain caterpillars have been made conspicuous for their own good, so as to be easily recognised by their enemies, on nearly the same principle that poisons are sold in coloured bottles by druggists for the good of man.

This tradition of studying associative generalizations and discriminations in natural settings is still vigorous as exemplified by the

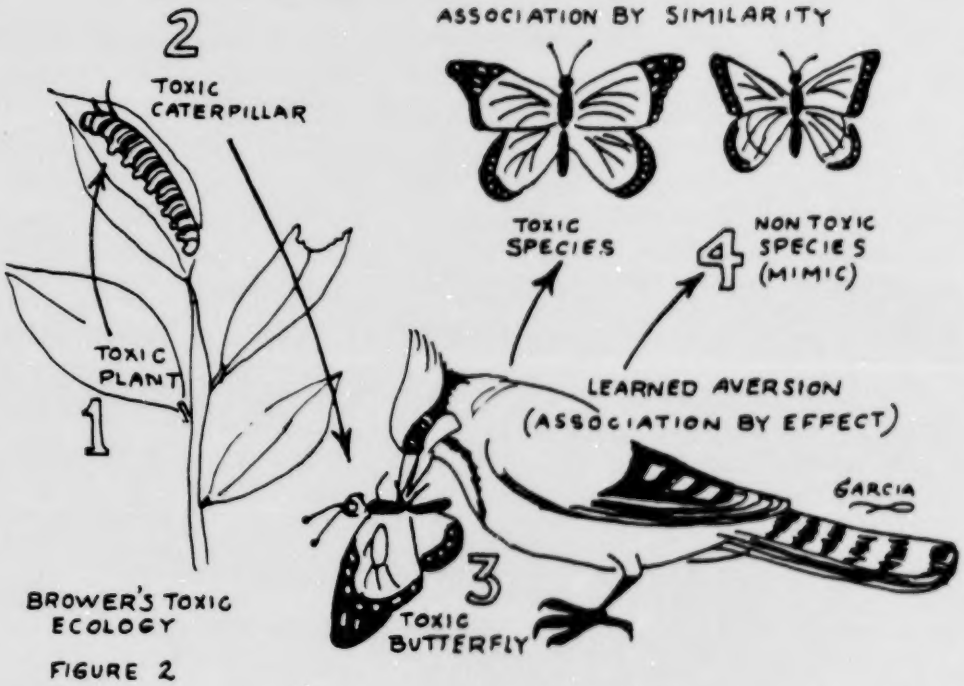

FIGURE 2

Figure 2 diagrams the acquisition of a taste aversion in a natural setting and the spread of the effect to visual cues. Through natural selection, the milkweed plant evolves a toxic defense against herbivores. The caterpillar consumes the leaves and sequesters the toxin in its exoskeleton for its own protection. The toxic caterpillar metamorphoses into a toxic Monarch butterfly. The bluejay eats a toxic Monarch and vomits, thus acquiring an aversive reaction to the taste and the visual patterns of the Monarch. The Bluejay also avoids the Viceroy butterfly which is a mimic of the Monarch. Learning is embedded in ecology (Brower, 1969).

research of Lincoln Brower (1969) who demonstrated that certain caterpillars feeding on toxic plants metamorphose into toxic Monarch butterflies. As illustrated in Figure 2, bluejays eating a toxic Monarch butterfly become sick and vomit, thereafter they avoid not only the Monarch buttefly but the Viceroy which mimics the Monarch in color and pattern.

This Darwinian conditioning model and its related line of research is rarely treated as such in texts and tomes of Psychology, although it is well represented in Biological volumes. However it is a well-documented learning theory. Furthermore it antidates the comparable conditioning theories of Pavlov (1903) and Thorndike (1911) by several decades. Perhaps Darwin's theory was overlooked because the subject under investigation did not learn the association in question. The caterpillar merely carried the warning signals and the punishing noxious effects. The caterpillar's "enemies", amphibians, reptiles, birds and mammals all considered together, did the learning. Nevertheless, Poulton clearly delineated the mechanism of associative learning in his comprehensive paper.

Pavlov and the Drooling Dog.

Ivan Petrovich Pavlov focused on the neural mechanisms within the brain of a learning organism (Principles IV and V). Consider his classic experiment: The sound of a bell is immediately followed by food. After repeated trials the dog salivates whenever the bell rings. This was hardly surprising, for as Pavlov said, others had observed it before. What made this trivial salivating act significant was its adaptive character and its neurophysiological integration. Dry food causes copious salivation; moist food causes little. Food induces a thick mucin lubricating a bolus for swallowing; vinegar induces a thin, watery saliva for flushing out the mouth

(see Figure 3). A smooth pebble induces little saliva, but when ground into sand it induces copious amounts, for while a pebble can be ejected without fluid, sand cannot. Pavlov (1903/1981) theorized:

> Here we have exact and constant facts--facts which seem to imply intelligence. But the entire mechanism of this intelligence is absolutely plain. On the one hand, physiology has long known about the centrifugal nerves of the salivary glands which now chiefly cause water to enter into the saliva and now accumulate in the saliva special organic substances. On the other hand, the internal lining of the oral cavity consists of separate areas which act as receptors for different special stimuli--mechanical chemical thermal...[where] the specific centripetal nerves have their origin...The above mentioned facts, on the one hand, provide certain and in my view important conclusions about the processes taking place in the central nervous system; and on the other hand, they make possible further successful analysis.

Pavlov was, afterall, a Darwinian physiologist who wanted to study intellectual behavior in an objective way; brain mechanisms were absolutely plain, that is, clear of the obscurities of idealistic mentalism. Conditioning was a method of establishing a new temporary association in the biopsyche of the dog. Before conditioning, the dog salivated at food, but did not salivate at the bell, therefore the brain center which received food stimuli controlled the salivary motor center while the auditory center did not. After conditioning, the dog salivated at the bell as if a new cortical pathway from the auditory center to the salivary center had been established by temporal contiguity (see Figure 3).

Thorndike and the Restless Cat.

As it was with Pavlov, so it was with Edward Lee Thorndike, at least in the beginning. Thorndike was also a Darwinian functionalist concerned with neurophysiologyical mechanisms. Consider his classic study: A cat is locked in a box containing a mechanical latch controlling the door. Food is outside. By accident, the cat trips the latch obtaining freedom and food. With

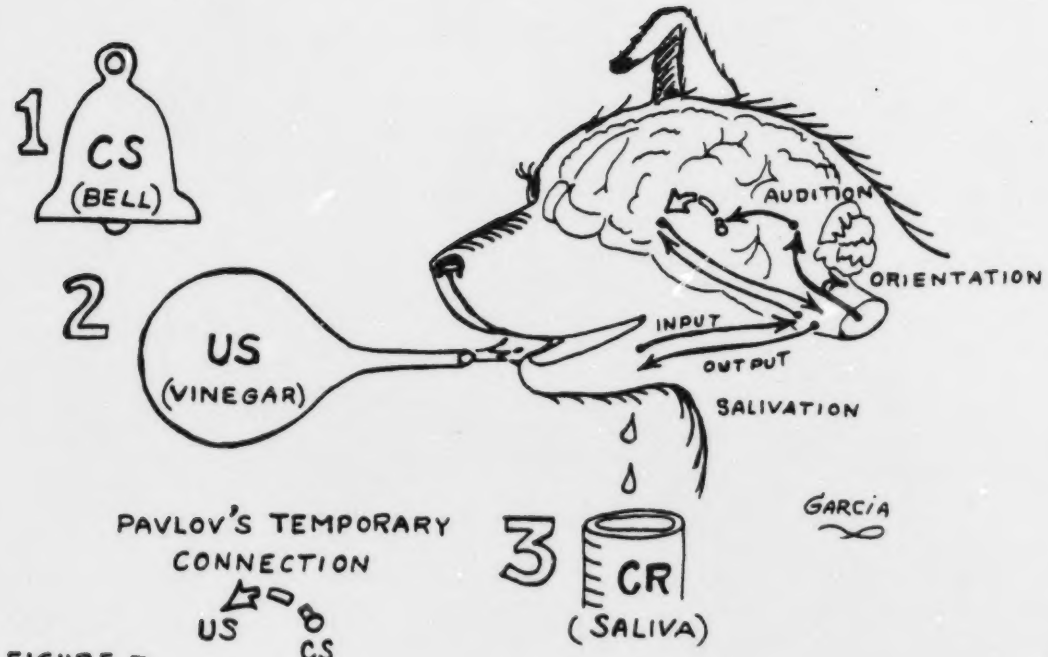

FIGURE 3

Figure 3 illustrates Pavlov's rationale. He selected a vinegar-like fluid to produce a reliable salivary reflex because he understood the neurology of that system. He selected an auditory stimulus (bell) because that stimulus caused the dog to pay attention (orient) but the bell did not cause the dog to salivate before training. After bell-vinegar training, the dog salivated at the sound of the bell. Pavlov argued that a new temporary connection had been established between the auditory system and the salivary system. That temporary brain process induced by learning was the critical issue in Pavlov's problem.

repeated trials, the cat uses the same response to free itself with increasing promptness. Nothing surprising in the cat's increasing skill, it must have been observed eons ago by neolithic pet-owners as they also witnessed the anticipatory salivation of their dogs. But Thorndike had a theory based on the cause and effect sequences described in Principle III. He called it the "Law of Effect". Of the various responses made in the closed box, the one closely followed by satisfaction to the animal will become firmly connected to the box situation. Describing satisfaction, Thorndike (1911) wrote:

> The satisfiers for any animal in a given condition cannot be determined with precision and surety save by observation. Food when hungry, society when lonesome, sleep when fatigued, relief from pain, are samples of the common occurrence that what favors the life of a species satisfies its individual members...The annoyers for any animals follow the rough rules that alterations of the animal's "natural" or "normal" activities--as by capture, starvation, solitude, or digestion--are intolerable.

Thus, Thorndike paid his debt to Darwin, but he was troubled by exceptions to the survival rule. Humans learn many bad habits, drug abuse, alcoholism, and over-eating to name a few, which do not promote survival. Thorndike (1911) explained:

> Upon examination it appears that the pernicious states of affairs which an animal welcomes are not pernicious at the time, to the neurones. We learn many bad habits, such as morphinism, because there is incomplete adaptation of all of the interests of the body-state to the temporary interests of its ruling class, the neurones...satisfaction and discomfort, welcoming and avoiding, thus seem to be related to the maintenance and hindrance of the life processes of the neurones rather than of the animal as a whole, and to the temporary rather than permanent maintenance and hindrance.

Like Pavlov, young Thorndike knew it is the mechanisms of the brain that control adaptation and intelligence. Neither survival of the species nor survival of the individual could explain self-destructive acts. His "law of effect" operated upon the "selfish neurone" to the detriment of the whole organism at times. These notions have an oddly modern ring; animals shock

themselves repeatedly in the brain when electrodes are implanted in the septal region as if specific neurones are being satisifed. Individual neurones respond to specifically complex precepts or numbers and pontifical neurones respond to categories and abstractions. Endogenous opiate-like endorphins and their antagonists are secreted there as well. Such agents may yet explain the deranged self-destruction that puzzled Thorndike.

CRITIQUE OF PURE BEHAVIORISM

In the beginning of the 20th Century, the scientific study of learning sprang from a Darwinian view of natural selection and adaptive structure. Then about thirty years later, a schism occurred. A competitive theory was proclaimed. The psychology of learning was separated from biology and became "pure behaviorism". Pavlov's and Thorndike's systems were stripped of both their adaptive implications and their neurophysiological mechanisms. Charismatic theoreticians, such as Watson (1925), Spence (1947) and Skinner (1966), offered psychologists marvelously simple programs for controlling the animal's behavior without need to study its natural ecological niche or its central nervous system.

The way that the behaviorists accepted the methods of Pavlov and Thorndike and stripped their systems of adaptive biology is reminescent of the way in which the empirical philosophers created the "mind" by stripping the "soul" of its medieval metaphysical rationalizations. But in this case, the study of learning was denied the genuine benefits of unification with the other <u>empirical</u> life sciences. Nevertheless, psychologists decided to go it alone. It was a mistake, a great mistake, but mistakes are part of the learning process, so this one must be critically reviewed.

<u>Eviserating the Organism</u>.

This stripping process culminated in B.F. Skinner's "behavioral engineering". In a series of position papers and a book entitled, Behavior of Organisms, Skinner (1938) offered us a simple system for controlling behavior based on economic theory. As profit operated in a free market to produce the required goods and service, so reinforcement would act upon a free organism to produce the required behavioral patterns. In this view, the organism had a repetoire of responses which it freely emitted, each at a given rate. In order to control the animal, Skinner applied a reinforcer immediately after the organism did what he wanted it to do. The reinforcer increased the rate of the chosen response. If the organism did not do exactly what Skinner wanted, he reinforced the responses which were most similar to the target response. As the organism repeated the similar responses with some variation, Skinner (1957) reinforced those variants which were even more similar to the target response. Gradually, the organism's behavior was "shaped" in the direction of the target behavior like clay in the hands of a sculptor according to Skinner. The reinforcer was both a guide to what the experimenter wanted and a pay-off for "correct" responding.

In order to clear the way for his new behaviorism, Skinner replaced the structured organism with an empty black box. He dismissed Pavlov's eliciting stimulus and its centripital neruones as well as Pavlov's evoked response with its centrifugal neurones. "The notion of a reflex is emptied of any connotation of the active push of the stimulus", he wrote, "It is studied as an event appearing spontaneously with a given frequency." Skinner also preferred to speak of a response as an "operant" stressing its operational effect on the environment rather than its intrinsic topography. For example, the important datum for a rat in Skinner's box is the excursion of the lever,

it does not matter whether the rat depresses the lever with its left paw, its right paw, its chin, or its rump, all methods yield the same environmental effect, the automatic advancement of the food delivery mechanism and the response counter. Some of our operant friends covered the "peekholes" in their Skinner boxes so that their students' concentration on the response counters would not be disrupted by observations of the rats or the pigeons in action.

Emptying the Reinforcer.

Thorndike's (1911) neural reinforcement was dismissed as well; Skinner's reinforcement worked on the whole organism without regard to internal hook-ups. The survival value of reinforcement and the satisfaction of the subject was no concern. The reinforcer was simply defined by the following test: Any stimulus applied immediately after an emitted response, which increases the frequency of that response is a reinforcer. Of course, no one applies this rule because it is too cumbersome. For example, some bats prefer the nectar of flowers and some prefer the blood of cattle, it is much simpler to find this out by observing bats in their natural habitat or examining their specialized oral structures, than to empirically offer an unknown bat an endless series of foodstuffs. In practice, operant conditioners merely select a pigeon or a rat, starve it 80% of its free-feeding weight and offer it the standard laboratory fare.

The empirical rule for defining the reinforcer makes more sense when an operant therapist is attempting to modify the behavior of inmates in a psychiatric ward. The therapist must carefully record the various responses of oddly behaving patients noting their frequencies, in doing so, he learns a good deal about patients. Juan Luis Vives would have approved. Then the

therapist can arrange a contingency between a low-freqency response, e.g. washing up and making the bed, and a high-frequency normal response, e.g. shopping in the commissary, and so the patient's behavior appears to be modified towards normalcy. But many patients are in the psychiatric wards because their idiosyncratic reinforcers are "abnormal" and cannot be applied ethically or legally. Other patients apparently respond to intrinsic reinforcement which can not be metered but by the therapist. Skinner, in effect, buried too many psychological problems in the empirical reinforcement rule. His method was limited because it failed to address the nature of reinforcement and because it provides no hypotheses for modifying reinforcers.

The final reduction of operant conditioning into a methodology completely empty of biological purpose was brought about by David Premack's (1965) probabilistic description of reinforcement. Consider a thirsty rat placed in an activity wheel connected to a water spout. Running responses are reinforced by water which promotes the rat's survival according to Thorndike's way of thinking. A thirsty rat running to water seems natural, but Premack said that this sequence is arbitrary. Water is neither a required substance, nor a reinforcing stimulus. Running and drinking were simply two operants, each with an empirical probability of occurring depending upon the situation arranged by the experimenter. If the experimenter deprives the rat of water, he simply makes drinking more probable than running and so the rat runs to drink. But, if the experimenter deprives the rat of exercise, the rat will drink in order to run. Premack demonstrated this phenomenon by giving satiated rats access to a running wheel if they licked at the spout of a water bottle. Similarly some children played in order to eat, others ate in order to play. Thus the distinction between operants and reinforcers was

eliminated. Operant reponses were now the only behavioral elements, probabilities of occurrence was their essential property, and contingency relationships established their association. The system is as empty of biological properties as classical celestial mechanics (mass, velocity, gravity, time and distance) is empty of geological properties. Pure behaviorism had reached its culmination.

Eliminating Biological Variation.

Skinner also rejected Darwin's biological variation as a necessary ingredient for learning theory. He rejected variation of responses displayed by a single organism saying, "I suggest that the dynamic properties of operant behavior may be studied in a single reflex." He also rejected the biological variation between species in this oft-quoted passage (1938). Describing the similar response patterns generated by different animals in a Skinner box on a fixed-interval schedule, he said:

> Pigeon, rat, monkey, which is which? It doesn't matter. Of course these species have behavioral repetoires which are as different as their anatomies. But once you have allowed for differences in the ways in which they make contact with the environment, and in the ways which they act upon the environment, what remains of their behavior shows astonishingly similar properties.

Apparently, it did not occur to Skinner that any method which cannot distinguish among pigeon, rat and monkey, has serious limitations, or that species differences in behavioral repetoires and environmental contacts are the central concern of psychology.

Skinner selected pecking by the pigeon as his single reflex to study the basic laws of operant behavior. It is necessary to describe his behavioral paradigm in some detail. A pigeon is starved until it is at 80% percent of its normal weight. It is placed in a Skinner box which has a small

translucent disc called the key. Whenever the key is illuminated any depression of the key will activate a mechanical feeder making grain available for a few moments on an experimental schedule. Note that Skinner's pigeon had to work for the food pay-off, while Pavlov's dog was presented with bell and vinegar, no matter how it behaved. This was a crucial difference between the two systems, or so it seemed. The Skinner box proved to be so convenient that all sorts of animals were placed in operant boxes, rats, cats, monkeys, and even dogs served as subjects.

Operant conditioning thrived for a while almost unchallenged. Complex "purposive" behavior directed at temporally and spatially distant goals was simulated by a chaining procedure in which operant elements are linked into long sequences. For example, a rat may be shaped into picking up a marble by immediate reinforcement, then carrying the marble to the foot of a stairs by a second shaping phase, then carrying it up a ladder by a third shaping stage, and so forth. Finally, the entire behavioral "compound" of picking up marbles, carrying them upstairs, and dropping them down a chute to operate a food delivery mechanism may be engineered. An innocent observer of the ultimate behavior sequence, unaware of the long history of shaping and chaining, might proclaim the rat's behavior to be purposive and intelligent, as he might also see purpose and intelligence in the mechanistic evolutionary process of random variation and natural selection. From a strictly Skinnerian point of view, intelligence and purpose is only a socially defined collection of operants in a chained sequence. Simply define those operants which you consider "intelligent" and reinforce them. This theory was put to practice in teaching machines and programmed courses of instruction.

The Return of Instinct

No sooner had the crowning touches been placed upon the elegant and empty edifice of operant conditioning, when Skinner's students and followers began to undermine its foundations. Keller and Marian Breland left the operant laboratory, well-trained in shaping and chaining responses, to establish a business training animals for amusement parks and television commercials. In the main, they were successful, but they had some difficulties which posed serious problems for operant theory. Take one familiar display as an example: A pig is conditioned to put a large wooden coin, or token, into a slot in its "piggy bank". The token trips a mechanism delivering food. In the beginning, the pig quickly picks up a token and drops it in the bank, runs back, picks up another token, banks it, and repeats the process until the food mechanism delivers reinforcement. After a few weeks, problems develop. The pig eagerly runs to pick up the token, but on the way to the bank it drops the token, roots it along the floor playing with it before reluctantly depositing it in the bank. The operantly conditioned "middle class" behavior is progressively replaced by "pig-like" behavior which delays, or eliminates, reinforcement in direct contradiction with operant principles. Making the pig hungrier does not eliminate the "pig-headed" behavior. The same thing occurred in pig after pig. The Brelands found it simpler to train a new pig than to rehabilitate an old one.

In a similar way, operantly conditioned behavior was disrupted by natural behavior in species after species. Cats left the manipulanda to stalk the food slot. Raccoons refused to deposit their tokens, rubbing and washing them instead. Chickens refused to operate the bat and pecked at the baseball. In the end, the Brelands turned away from arbitrary operants and reinforced natural acts instead: Scratching chickens were trained to "dance" and

dabbling ducks were trained to "play the piano" with their bills, but their roles could not be easily reversed. Breland and Breland (1961) told it all in an article entitled "The Misbehavior of Organisms", obviously aimed at their mentor. Operantly engineered behavior, they said, drifted back towards the unconditioned behavioral repertoire of the species.

The Cat Behind the Glass Door.

The return of instinct, now called "species-specific behavior", to psychological explanations of learning is exemplified by two similar experiments separated by a third of a century. In the original version, Guthrie and Horton (1946) confined a cat in a puzzle-box behind a glass door. The glass door could be opened by jostling a vertical rod, approximately 12 inches tall, standing upright about 12 inches from the door. Cats placed in the box one after the other, rubbed up against the rod, and released themselves in a stereotypic manner.

Guthrie's explanation of the cat's behavior was an ingenious example of pure behaviorism. On the first trial the cat "accidentally" rubbed against the rod and was immediately released, so it made no further "box responses" to interfere with the memory of rubbing the rod. When the cat was returned to the box, it retrieved the memory of the last "box response" and repeated the rubbing behavior. The box stimuli and the rubbing response were thus welded together by contiguity in time and space; the cat lacked "insight" into the lever mechanism, so it repeated itself in a blind superstitious manner. Guthrie offered this general explanation: the last coping response is always learned because reinforcement takes the organism out of the problem situation; food ends hunger responses, water ends thirst responses and sex ends courting responses. Guthrie's hypothesis was not completely different from Premack's

or Skinner's explanations.

Moore and Stuttart (1979) repeated the study with a slight variation. The rod was disconnected from the door so that the cats could not release themselves. Nevertheless, their cats rubbed the rod just as Guthrie and Horton's cats did many cat generations before. However, when Moore and Stuttart absented themselves from the cats' view, the cats stopped rubbing. When they returned, the cats rubbed on the rod again. The cats were greeting Moore and Stuttart as the prior cats had greeted Guthrie and Horton. Rubbing was not learned nor reinforced in either experiment.

Moore and Stuttard pointed out that many members of Felidae, including lions, tigers, jaguars, ocelots and domestic cats display flank-rubbing and head-rubbing during greeting rituals and courtship. Typically, one cat moves sinuously past another, brushing the object of its affection with its back arched and tail held high. Alternatively, when the other cat is not within reach, the cat will rub itself sensuously against inanimate objects such as vertical rods. Domestic cats will greet humans the same way, as if they were conspecifics. The behavior is one of those stereotypic patterns which can be used to phylogenetically classify an organism.

When a conditioning program runs counter to species-specific behavior the animal may fail to perform even though it may learn the required association. Linda Brett (personal communication, 1976) told us of her attempts to increase the growling responses of a polar bear with food reinforcement. Presumably, the bear growls menacingly to drive away competitors and rivals in the wild. When the bear began to associate Brett and food, it became understandably reluctant to growl and threaten its source of food. But it seemed to recognize that vocalizations were required. Brett said the confused animal

made some weird sounds in its effort to cope. Failure to growl on cue was not an indication of failure to associate; to growl appropriately, the bear would have to be trained to control its emotions like a "method" actor.

The Pigeon's Dilemma in Skinner's Box.

Ultimately, Skinner paid the price for dismissing Pavlovian mechanisms in an ironic way. As Bruce Moore (1973) effectively argued, the pigeon's key-peck was not a freely-emitted operant, nor was it shaped by Skinner. The peck is a Pavlovian response evoked by the lighted key. Observations of the pigeon's key-peck with slow-motion film techniques indicated that, like Pavlov's dog salivating at conditioned stimulus (CS), the pigeon was directing consummatory responses towards the lighted key. When the key-light was paired with food, the pigeon pecked at the key as if it were grain. When the key-light was paired with water, the pigeon acted as if it were trying to drink the key.

Brown and Jenkins (1968) altered the Skinner box in a simple yet theoretically significant way. They merely lit the key and then made the food available at a fixed time later, no matter what the pigeon did. As under social welfare, there was no obligation to work the key, the bird could simply eat the food. Actually this is a Pavlovian arrangement, the key light is the conditioned stimulus (CS) which elicits orientation and food is the unconditioned stimulus (UCS) which elicits pecking, the unconditioned response (UR). And as Pavlov would have predicted, the pigeon first pecked at the food, but after repeated light-food pairings it began to peck at the lighted key just as his dog came to salivate at the bell which was paired with food. Pecking was a conditioned response (CR). Staddon and Simmelhag (1971) gave their pigeons free grain every twelve seconds and the pigeons oriented towards

the feeder pecking at the nearby wall. After a time they demonstrated temporal discrimination, pecking at the end of each twelve second interval when gain was imminent. The general phenomena, called "autoshaping" as opposed to "experimenter-shaping", was verified in other species.

William and Williams (1969) took auto-shaping one step further, they withheld reinforcement whenever the pigeon pecked the lighted key. That is, grain not presented if the pigeon pecked at the key, on the other hand, grain was presented if the pigeon refrained from pecking the lighted key. Nevertheless, many pigeons continued to peck at the key for hundreds of trials. The pigeon is not stupid, its pecking response is as "involuntary" as the dog's salivary response, or yours for that matter. Consider yourself to be the subject of such an omission-training auto-shaping experiment. You are ravenously hungry, I show you a plate of your favorite food, all you have to do in order to eat is to refrain from salivating!

The pigeon is a marvelously adaptive creature capable of making fine discriminations. It can cope with time and distance displaying a sophisticated learning capacity for navigation as it forages for food and returns to its loft. But once it begins to eat, plasticity is limited. As illustrated in Figure 4, in its natural niche, a seed offers the pigeon; (1) the occasion to peck, (2) the target to peck, and (3) the reinforcement for pecking. The Skinner box breaks up that natural seed packet into three arbitrary components. The light signals the occasion, the key provides the target, and the food cup provides the reinforcement for pecking. When these three factors are clustered in close spatiotemporal proximity, as they were in the original Skinner box, then the pigeon adapts effectively. But if the three factors are widely separated, the pigeon is relatively helpless. It

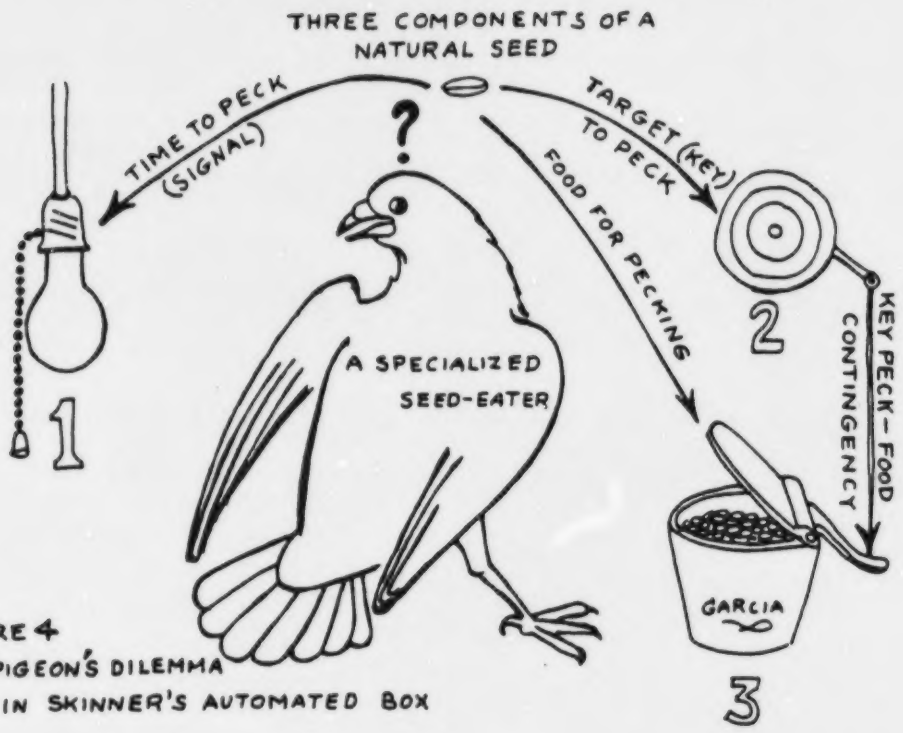

FIGURE 4
THE PIGEON'S DILEMMA
IN SKINNER'S AUTOMATED BOX

Figure 4 illustrates the difficulties encountered by a pigeon in a Skinner box. In the natural world, the seed provides the signal to peck, the target to peck and the reward for pecking. As long as these three components are clustered together in one place, the pigeon is effective. However, the pigeon finds it extremely difficult to look at one signal and to peck at another target in order to get food at a third place. If the signal is presented on the target, the pigeon will readily peck at the signal-target, but it has difficulty in learning not to peck at the signal-target in order to obtain food. If the signal-target and food delivery are paired, with the keypeck-food contingency disconnected, the bird will peck at the signal-target nevertheless. When food is imminent, the hungry pigeon pecks just as the hungry dog salivates (Moore, 1973).

simply cannot watch for a signal to peck in one place, peck at a different place, and receive its food from in yet another place. The seed of its natural niche has been pulled apart far beyond the pigeon's capacity to adapt.

The degree of learning involved in instrumental responses beginning the behavioral seqence of a pigeon and the consummatory reactions ending it was discussed by Wallace Craig (1917) long before the advent of operant conditioning as follows:

> An appetite is accompanied by a certain <u>readiness to act</u>. When most fully predetermined, this has the form of a chain reflex. But in the case of most supposedly innate chain reflexes, the reactions of the beginning or the middle part of the series are not innate, or not completely innate, but must be learned by trial. The end action of the series, the consummatory action, is always innate.

THE SELECTIVE PRESSURE OF THE FOOD CHAIN

Charles Darwin noted that everything that was born, was bound to eat--and to be eaten. Plants are eaten by herbivores, herbivores are eaten by carnivores and carnivores are eaten by scavengers. The wastes from feeding and dying returns to feed the plants. The food chain is more like a vast fabric which includes tiny creatures, bacteria, biting insects, internal parasites and dung beetles as well as the larger animals. To forestall extinction, each animal must delay the final alternative until it has eaten and reproduced, thus the food chain exerts a powerful selective pressure on the evolution of corporal structure, instinctive behavior and learning mechanisms.

Even plants resist being eaten employing germicides, pesticides and appetite suppressors. Many herbivorous insects utilize plant poisons for their own defense, as illustrated in Figure 2. Humans also utilize plant toxins for their own purposes. Quinine and other alkaloids are extracted from the bitter cinchona bark of trees and introduced into human blood to resist

the ravages of malarial parasites. Digitalis, a genus of herbs including foxglove, contains important glycocides and serves human cardiovascular patients as a heart stimulant. The glycocides serve the herbs by turning off the appetite of the herbivores. Caffeine is extracted from coffee beans and used to suppress appetite and promote diuresis in those wishing to retain a slim, fashionable figure. Caffeine is also used to excite the central nervous system acting as an anti-depressant. In nature, it may make the animal too excited to eat. The most common complaint of those who stop smoking is that they gain weight, so nicotine also probably works to excite nervous activity and suppress appetite. In addition, nicotine is used as an insecticide, a role it also plays in nature. Natural herbs are used all over the world for medicinal purposes, but it must be remembered that herbal chemicals evolved to promote the survival of the herbs, they are not as nature's gift to humans.

All of this chemical warfare in the plant kingdom and in the first links of the food chain present the intermediate feeders with food selection problems. Meanwhile larger predators always on the hunt for meat, pose a second safety problem for the feeder caught in the middle. All species occupy this vulnerable intermediate position in the food chain, or occupied it at some point in their phylogeny. In a similar way, all individuals occupy the same middle position, or occupied it at some point in their ontogony. Thus, all animals have evolved two defense systems, one to protect their gut from poison and the other to defend their skin from predators (Garcia, Forthman Quick, & White, 1984; Garcia, Lasiter, Bermudez-Rattoni, & Deems, in press).

Body and Brain.

The dichotomous structure of the feeder in the middle is illustrated in Figure 5. A salamander is represented, but all vertebrates possess the same

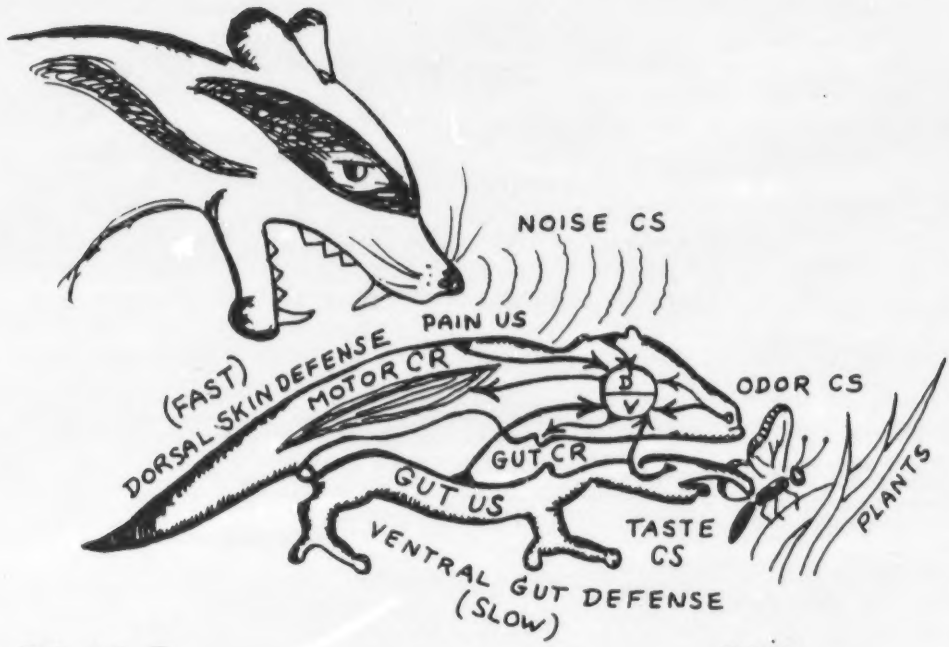

FIGURE 5
HERRICK'SALAMANDER
TO EAT -- OR -- TO BE EATEN?

Figure 5 depicts natural selection pressure inherent in the food chain and its effect upon the body and brain of the salamander and other vertebrates. The brain is divided into two systems. Distal noises and proximal insults protect the skin against predatory attack. The output from these mechanisms converge to dorsal brain mechanisms engaging striated muscular reactions of avoidance and escape. Food taste and visceral feedback from consumption converge to mechanisms in the ventral regions of the brain where taste preferences are established commensurate with food effects. The output of this system is to the smooth muscles of the gastrointestinal tract. Olfaction (and vision) can be used in either the dorsal or ventral systems (Herrick, 1948).

general body plan. The gut for processing food, essentially a long tube lined with sensors and fitted with sphincters at both ends, occupies a ventral position in the body. Digestion is a comparatively sluggish process attended by glandular secretions and smooth muscle actions. The taste receptors of the oral end of the tube provide the CS by chemical analysis of the food. The visceral receptors of the mid-gut report on the effects of the food thus providing the US in a conditioning sequence. If the food is bitter it is usually rejected at the mouth. If a toxin enters the system, it may be ejected by vomiting or speeded on its way out by diarrhea. Gut-defense is only one subsystem within the larger homeostatic system protecting the internal environment.

Skin-defense is essentially a motor system designed for escape, replete with "early-warning" alarms and proximal damage sensors, located in the dorsal aspect of the body. Since the attack of the predator is sudden and swift, skin-defense is characterized by fast striated-muscular motor reactions. Although vision and olfaction provide excellent distal cues, they tend to be directional and possess "blind spots". In most vertebrates, the audition is the principle warning system picking up signals from all around the organism and remaining on guard during rest and sleep. It is no accident that our own mechanical alarms emit noisy vibrations and that visual signs point to escape routes. Skin defense is only one subsystem within the greater external system designed to cope with the external environment.

The mouth plays a pivotal role in both external and internal systems. After the vertebrate feeder arises from its rest, its first reaction is to examine its immediate surroundings for danger. If all is well, the animal forages for food in the external world, thus food acts as a Thorndikian

reinforcement for the instrumental phase of the feeding sequence. Feeding cues act as CSs and food in the mouth acts as a Pavlovian UCS in the consummatory phase. We have added a third homeostatic, or Darwinian, phase. Food in the mouth acts as a CS and the effects of food on the gut act as the UCS. The homeostatic food UCS can operate in both directions; toxin is a negative UCS while nutrition is a positive UCS.

The dorsal-ventral duality so obvious in the vertebrate body is also reflected in the organization of the brain. C. Judson Herrick (1948) describes it most eloquently:

> Precise localization of function stops at this place where the peripheral nerve fibers make contact with the central nerve cells in a dense feltwork of interlaced fibers, termed neuropil. One of these pools--the visceral sensory neuropil associated with the fasciculus solitaris--receives all fibers of gustatory and general visceral sensibility and discharges into the visceral motor mechanisms. the other pool--the somatic sensory neuropil--receives fibers of all types of cutaneous and deep sensibility that are concerned with adjustment to the external environment, i.e., the exteroceptive and proprioceptive systems of Sherrington's analysis. This neuropil discharges into somatic motor apparatus that controls the movements of the skeletal system.
>
> This segregation of all sensory nerve fibers, except those of vision and olfaction, into only two receptive centers is the only well-defined localization of sensory functions present in the medulla oblongata. It corresponds with the fundamental difference in behavior between internal visceral activities and somatic sensorimotor activities that have an external reference. The visceral movements are for the most part of total pattern type. This is as true in men as in salamanders. Accordingly, there is little more specialization or separate localization of function in the fasiculus solitarius neuropil of men than of salamanders.

Prey and Predator.

Some odd behavior results when incompatable conditioning has taken place in the external and internal systems of a wild predator. Figure 6 provides one example of a confused wolf. Several days before, the wolf was given a mutton "burger" containing capsules of lithium-chloride. The wolf bolted down

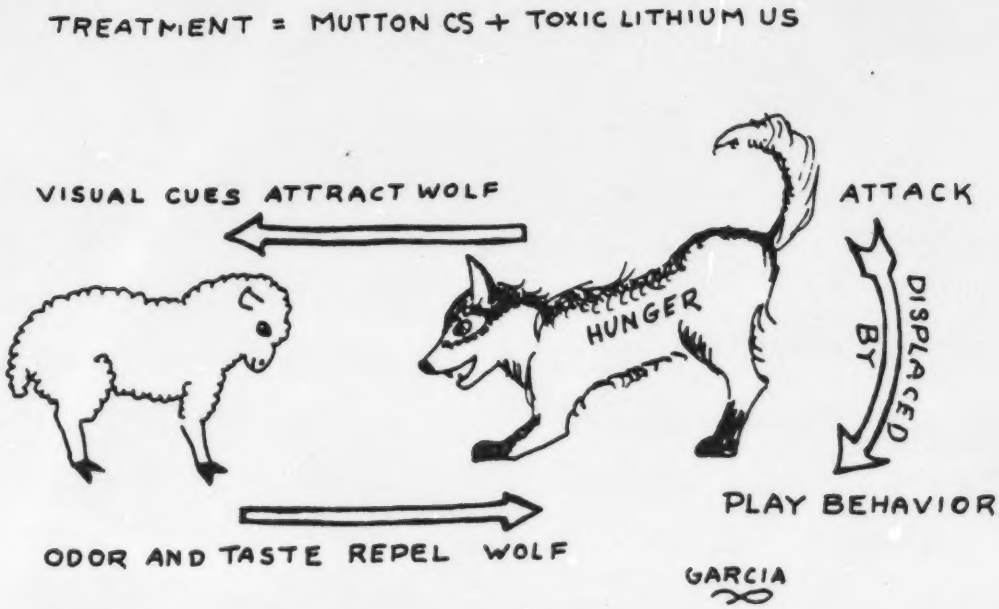

FIGURE 6
THE WOLF'S DILEMMA AFTER TOXICOSIS

Figure 6. Previously, the wolf was given some mutton laced with lithium chloride; about a half hour later, it retched and vomited. When confronted by its customary prey, the wolf was attracted by the visual aspects of a possible meal, but repelled by the odor and taste of the sheep. As a result of this conflict, the behavioral attack pattern of this canid species was replaced by another species-specific pattern, i.e., an invitation to play (Gustavson et al., 1976).

everything. It is important to note that the wolf did not smell or taste the lithium chloride enclosed in tasteless capsules which were swallowed whole. And that the mutton burger smells and tastes like a sheep, but does not look like a live sheep. About a half hour later, the wolf became sick and vomited then recovered rapidly (Gustavson, Kelly, Sweeney, & Garcia, 1976).

Several days later a sheep was let into the wolf's compound. The hungry wolf charged eagerly, ears up and tail carried high like a cavalier's plume. It went for the throat burying its muzzle in the wool of its prey, then abruptly broke off the attack. Circling its potential victim, the wolf attempted a hamstring attack but again it recoiled as soon as it made contact. Then, continuously orienting to the sheep, the wolf circled again and again, obviously reluctant to close with its prey. As the hour-long test wore on, the distance between the predator and its prey increased and the behavior of both animals changed dramatically. The sheep began to make short charges, lowering its wooly head as if it bore horns. The wolf dodged and made submissive species-specific gestures. It bowed like canine puppies bow, head and thorax on the ground, rump in the air, inviting the sheep to play (see Figure 6). It never attacked again. When a rabbit was introduced into the pen, the wolf immediately killed and ate it. After feeding, the wolf no longer paid attention to the sheep acting as if its former prey no longer existed.

As a result of the mutton-lithium treatment, the wolf had acquired an aversion for the odor and taste of the sheep, but no aversion for the vision of the sheep, presumably because the poisoned mutton did not resemble the living sheep. The wolf was in conflict visually attracted to the sheep but repelled by its odor and taste. It resolved the conflict by treating its

former prey as if it were a dominant conspecific. Attack behavior was displaced by social play behavior. When the wolf's hunger was satisfied by rabbit flesh, the curious social contract between prey and predator was dissolved, the wolf ignored the sheep and the sheep ignored the wolf. Another wolf tested at the same time responded in the same way (Gustavson et al., 1976).

Figure 7 provides a second example of the curious behavior of avian predators poisoned after eating the flesh of their natural prey. In contrast to the wolf, the hawk normally searches for prey with its keen vision from high in the air, then swopes to kill with taloned feet, never tasting the prey in the instrumental phase. In captivity, our broad-winged hawks were normally fed white mice as a necessary part of their diet. On conditioning trials, the first hawk was given a black mouse and later injected with a lithium chloride solution. Since the hawk was accustomed to eating mice it had no discriminatory taste cue for the injected poison but it had an excellent visual cue. Several days later, when the hawk was tested with black and white mice, it ate them both with no sign of discrimination. When the two more black-poison conditioning trials were imposed, the hawk refused both black and white mice. The hawk had a taste aversion for mouse flesh but no visual aversion for black mice.

A second red-tailed hawk was conditioned the same way except that the black mouse was dipped into a mildly bitter solution. The hawk ate the black bitter mouse without undue hesitation. Several days later, an identical black mouse was placed on the floor of the large cage with the hawk on its perch four feet above. The hawk looked down, "smacked" its beak but refused to strike. Efforts to tease the hawk into action by moving the dead mouse were

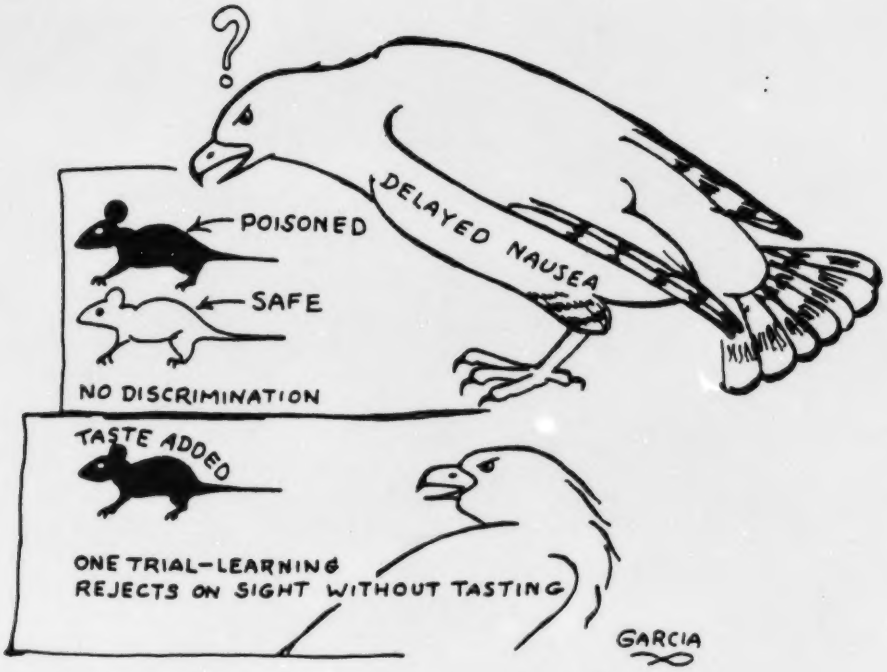

FIGURE 7 THE REDTAIL HAWKS AND THE TAINTED MICE

Figure 7. What an animal cannot learn is often more informative than what it can learn. Hawks fed on a diet of white mice, and occasionally given a black mouse followed by an emetic injection, cannot learn to discriminate black from white, presumably because both mice taste the same. When a distinctive taste is added to the black mouse, the hawk learns to avoid black mice on sight after a single black mouse--emesis episode. The taste cue has potentiated the color cue (Brett et al., 1976).

of no avail, it merely looked and smacked its beak. Apparently the black mouse was evoking conditioned illness in the hawk because "beak smacking" is a symptom of nausea. When Brett picked up the black mouse and placed it on the perch, the hawk retreated in obvious disgust. The second hawk had a visal aversion as well as a taste aversion.

A third hawk was conditioned the same way, except that a white bitter mouse was paired with the lithium injection. Thus, this hawk, not included in Figure 7, had a taste cue but not a color cue. In the test, it seized the second white bitter mouse in its talons, but on tasting it, the bird refused to eat. The third hawk had a taste aversion for bitter but no visual aversion. Three other hawks tested under the same three conditions acted essentially the same way (Brett, Hankins, & Garcia, 1976).

The hawk experiments yielded a new empirical finding with broad theoretical implications. The first hawk demonstrated that black coat color, used alone, was a weak CS for a toxic UCS. The third hawk proved that bitter flavor, used alone, was a strong CS under the same conditions. According to Classical learning theory, when a strong CS and a weak CS are combined into a compound CS, the strong component should block conditioning to the weak component. This makes sense; if a strong cue is available, why bother with weak cues. Much evidence has been accumulated for this principle called "overshadowing" or "blocking" (Kamin, 1969). However, in the hawk experiment, the strong bitter cue potentiated conditioning to the weak color cue. Significantly, all of the evidence for blocking comes from conditioning in the external sphere, while the evidence for potentiation came from the hawk experiment dealing with internal homeostatic conditioning. (For a general review of the studies with wolves, coyotes and hawks, see Garcia & Brett,

1977.)

The Memory for Poison

The dual organization of the vertebrate brain is best illustrated by a series of behavioral experiments on the rat. Essentially the method is simply Pavlovian; present the rat with a variety of cues, induce a mild bout of nausea with a toxic treatment, then test the rat with each cue separately to see which cues the rat treats as poison. If a rat is given a drink with a novel saccharin taste and becomes nauseous an hour later, it acquires an aversion for saccharin. If it is given a drink of plain water in a novel compartment followed by the same treatment it is not likely to acquire a strong aversion for the novel compartment.

People display the same sort of selective learning and memory because, as Herrick describes above, they possess similar neural systems for control of feeding. If we become ill after a novel meal, we blame the food not the new wallpaper - on the dining room wall. This reaction seems cognitive and rational, but it is not. As any ship's steward knows, when the seas become stormy, the bilious voyager will first blame the food not the sea. After a bout of sea sickness, the passenger may have fond memories of the ship and long for the sea again, but the passenger will retain a strong aversion for the sardine lunch eaten just before the storm, knowing full well that the storm not the sardines caused the nausea. The ship's rat eating the sardine scraps in the hold will display the same pattern of aversions, but perhaps not the same cognitions. Radiation and chemical treatment for cancer often produce nausea in patients and the resultant patterns of aversions resemble those displayed by the Laboratory animal as we have discussed previously in an extensive review of the problem (Garcia y Robertson & Garcia, in press).

Many people think that the flavor of a food is mostly smell rather than taste. A heavy cold clogging the nose with mucous will destroy a good meal, it is often said, proving that olfaction is more important than gustation in the appreciation of food flavor. Recent experiments in the rat revealed that odor and taste play completely different roles in feeding behavior but that taste is the prime arbiter of what is fit to eat. As such, taste designates specific olfactory and visual stimuli to act as food-cues for the delayed effects of the meal. Garcia and Rusiniak (1980) have discussed this relationship in a paper entitled "What the nose learns from the mouth". Their paper also describes "what the bird's eye learns from its beak". We will now summarize the interaction of odor and taste in gut defense and skin defense.

Figure 8 illustrates half of the results obtained in a recent study demonstrating the utilization of odor cues in gut defense. Thirsty rats were habitually given their daily ration of water in an experimental apparatus where every lick at a water spout was recorded. The spout protruded through a "nose cone" where an odor was presented as scheduled. Taste was presented in the water according to the experimental schedule. Care was taken to prevent the rat from tasting the odorant or smelling the tastant. On the conditioning days, the drinking spout was marked with the novel taste and/or odor cues. One half hour later, rats were intubated with a mild dose of lithium chloride producing obvious malaise. The rats recovered in a few hours. Several days later, they were tested with the odor and taste cues administered in separate tests (Rusiniak, Palmerino, Rice, Forthman, & Garcia, 1982).

The "scoreboard" in Figure 8 summarizes the groups, their treatment and the results of the test. When taste alone is used as the CS, the rats acquired a taste aversion. When odor alone is used as the CS, the rats did

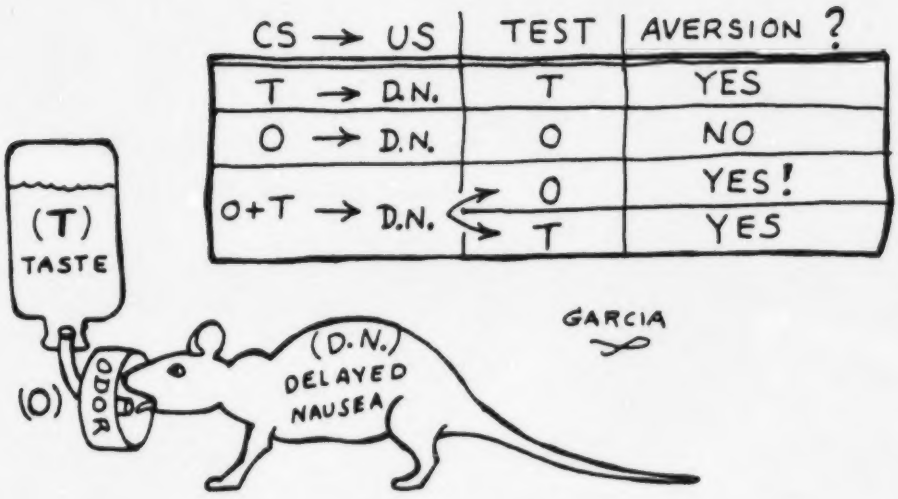

FIGURE 8. POTENTIATION

THE MEMORY OF THE POISONED RAT

Figure 8 presents a "scoreboard" with the results obtained in rats given a drink marked with taste and/or odor cues followed 30 minutes later by an emetic treatment. If odor is used alone, the rat does not acquire an odor aversion. If taste is used alone, the rat acquires a taste aversion. If odor and taste cues are used in combination, then the rat acquires an aversion for odor as well as taste. Taste has potentiated odor. Compare these results with those obtained in Figure 9 where rats received immediate foot shock. Note also the explanation offered in Figure 10 (Rusiniak et al. 1982).

not acquire an odor aversion. However, when odor and taste are combined and used as a compound CS, the odor component proves to be extremely aversive when tested alone. The taste component is also aversive but not more than when taste alone served as the CS. As in the case with the broad-wing hawks depicted in Figure 7, the stronger taste cue potentiated the weaker odor cue in direct contradiction to the classsic theory of overshadowing or blocking.

The Memory for Pain

The other half of the experiment demonstrating the utilization of odor cues in skin defense is illustrated in Figure 9. The experimental set-up was exactly the same, except for the reinforcement conditions. These rats received an immediate foot-shock for drinking instead of the delayed-illness treatment. Foot-shock and poisons both suppress drinking responses in the Skinnerian sense, but the two punishments are completely different in every other regard. Foot-shock is a sharp external insult coming from the floor, while nausea is a dull internal malaise stemming from the very guts. Shock produces fear of a place on the floor, nausea does not. To strip events of their biopsychological manifestations was Skinner's error. It was also Hume's error, when he argued that causality could not be differentiated from contiguity.

The scoreboard in Figure 9 gives the results of the shock experiments which stand in opposition to the poison experiments shown in Figure 8. When taste alone is followed by immediate shock, taste does not become fearful and the rat drinks the tasty water in the test. When odor alone is followed by shock, odor becomes fearful and the rat suppresses its drinking. When combined odor and taste are followed by shock, the taste component blocks conditioning to the odor component. But this is not the blocking effect

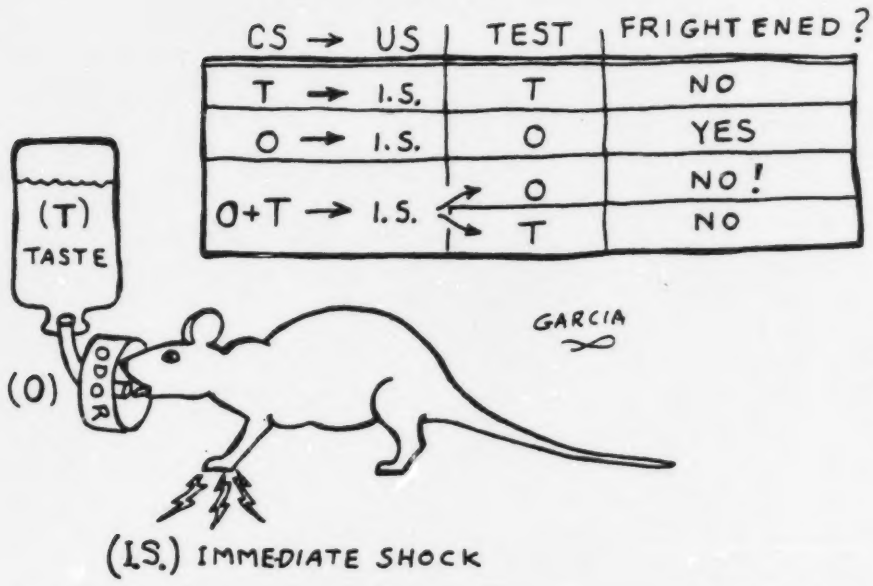

FIGURE 9. BLOCKING

THE MEMORY OF THE FRIGHTENED RAT

Figure 9 presents a "scoreboard" with the results obtained in rats given a drink marked with taste and/or odor cues followed a few seconds later by mild shock to the feet. If taste is used alone, the rat acquires no fear of the taste. If odor is used alone, the rat acquires a fear of the odor. If odor and taste are used in combination, the rat does not acquire a fear of the taste or the odor. Taste has blocked odor. Compare these results with those obtained in Figure 8 with rats receiving delayed emetic treatment. Note also the explanation offered in Figure 10 (Rusiniak et al., 1982).

described by Kamin (1969). Recall that in the classic blocking case, the strong component of a compound CS blocks conditioning to the weak component. However, in this case, the scoreboard indicates that odor alone is the stronger cue and taste alone is the weaker cue, so the weak component blocked conditioning to the strong component.

The Bicameral Biopsyche

A hypothetical explanation of the effects of poison, as opposed to pain, is graphically presented in Figure 10. Herrick's dual organization is again represented, but this time in the general form of the rat brain. However, this is not a "road map" of the rat brain, it is simply a schema to organize a good deal of behavioral and brain lesion data.

Auditory and cutaneous receptors have a common evolutionary origin and possess many similar functional properties. Afferents from both systems converge to the thalamus and then course rostrally to the limbic system and the cortex. These are the primary components of the skin defense system depicted in the dorsal aspects of Figure 10. On the other hand, taste and visceral receptors have a similar evolutionary origin in the lining of the primitive gut. Afferents from these two systems converge to the nucleus of the solitary tract in the brainstem, and then the two afferent systems course together via the parabrachial area to the gustatory thalamic relay, the limbic system and the gustatory neocortex. They form the principle components of the gut-defense system depicted in the ventral aspect of Figure 10. A more detailed description of this anatomy can be found in Braun, Lasiter, and Kiefer (1982).

The skin-defense and gut-defense systems as depicted in Figure 10 are separated by reciprocal inhibition, but also integrated by a sensory gate.

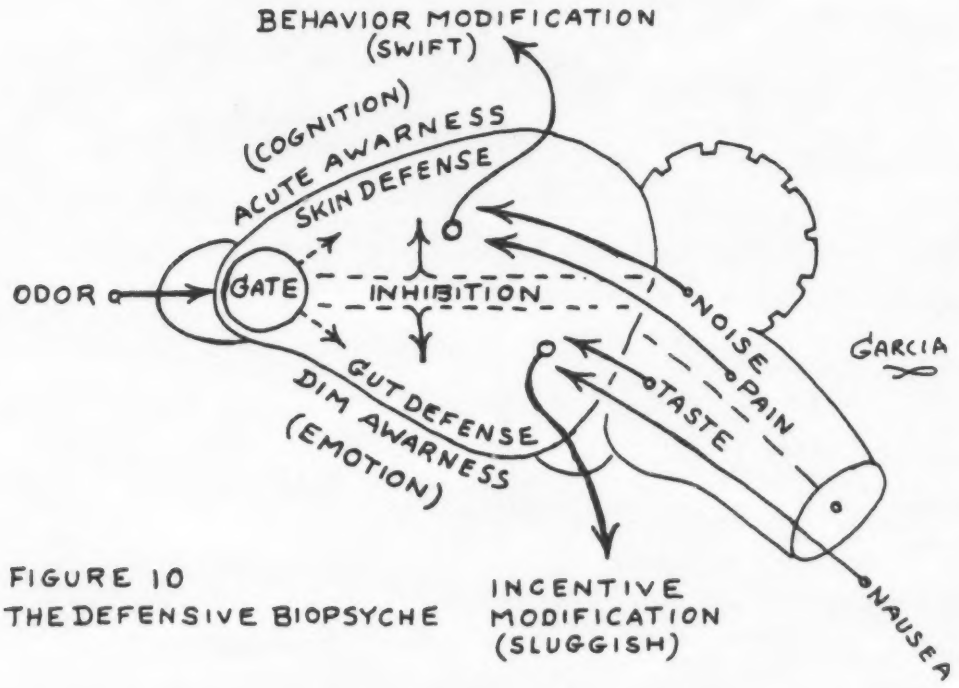

FIGURE 10
THE DEFENSIVE BIOPSYCHE

Figure 10 depicts an elaboration of the schema presented in Figure 5. It is an explanation of the results shown on the scoreboards of Figures 8 and 9. Noise and immediate shock enter the dorsal brain areas to modify behavioral patterns of skin-defense. Taste and delayed nausea enter the ventral brain areas to modify incentive value of food commensurate with food effects in defense of the gut. Fast reactions, acute awareness and cognition are characteristic of skin-defense. Sluggish reactions, dim awareness, and emotion characterize gut-defense. Odor enters either system: When taste is absent, odor enters the dorsal mechanism. When taste is present, odor enters the gut-defense. Test the implications of the gate with the results shown in Figures 8 and 9. Construct a similar explanation for the behavior of the hawk in Figure 7.

The reciprocal inhibition simply reflects the common observation that vertebrate organisms tend to allocate energy as needed, to one or the other of the two systems. After a heavy meal, digestion is promoted by visceral smooth muscle and glandular activity; striated muscles are relaxed, high amplitude slow waves sweep over the cortex and the organism prepares for sleep. Alternatively, if an alarm sounds, excitement reigns in skin-defense, while appetite vanishes and gastric stasis ensues in the visceral system.

Herrick (1948) in his description of the segregation of function in the amphibian brain excluded olfaction and vision from his two great neural pools in the medulla oblongata. Significantly, it was in these two systems that potentiation was discovered, as illustrated in Figure 7 and 8. Potentiation has been more extensively studied in the olfactory system of the rat, and accordingly is depicted in Figure 10. The experiments that revealed the action of the putative sensory gate utilized one, or at most three trials; this is important, for if many trials are used, the animal will undoubtedly devise complex behavioral strategies involving circuitous neural routes thus obscuring the gating action. Normally, the sensory gate is open to skin-defense and closed to gut-defense. Thus odor alone is an excellent cue for peripheral pain, but not internal malaise. When the rat is in a feeding set, induced by taste or some other feeding stimulus, the gate opens to gut-defense and closes to skin-defense, thus odor attended by taste is a good cue for malaise but a poor cue for pain. A sensory gate can also be invoked to explain visual potentiation in poisoned animals. Note that the gating hypothesis can also explain general blocking and overshadowing data as well.

A series of lesion and pharmacological studies indicate that a complex neural structure near the solitary nucleus, called the emetic system, is

involved in gut-defense. The effects of ingested poison are carried to this complex via two routes. First, the vagus nerve reports on the effects of local gastric irritation. Vagotomy will disrupt taste aversions induced by copper sulphate which is not readily absorbed in the blood. Second, toxins in the blood are monitored by receptors in the area postrema near the solitary nucleus, thus taste aversions induced by blood-borne toxins are disrupted by lesions of the area postrema, but not by vagotomy. The sensory gating mechanism is apparently located in the limbic system and the lateral aspect of the forebrain cortex. Pharmacological agents applied to the amygdala or the hippocampus have selective effects upon potentiated odor aversions, but not upon taste aversions, nor upon odor-shock avoidance responses. Punctate lesions in the upper part of the gustatory neocortex in the lateral forebrain will disrupt taste aversions but, oddly enough, spare taste potentiation of odor. Punctate lesions, a few millimeters lower, will disrupt conditioning to both odor and taste components. In short, the model displayed in Figure 10 has been supported by empirical exploration of the rat brain (Garcia, Kiefer, Rusiniak, & Bermudez-Rattoni, 1982; Garcia et al., in press).

Behavior modification in time and space of the external world is characterized by associations spanning relatively brief interstimulus intervals. For optimal learning, noise must be followed promptly by peripheral pain in classical conditioning and the rat's reaction times are also brief. Likewise, responses must be followed promptly by reinforcers in instrumental conditioning. In the external world, the vertebrate organism is acutely aware of its stimulus surroundings. It orients to signals and responses precisely to reinforcers. Subsequently, the organism will display a memory for the locus of the reinforcer in space and for the temporal

relationship between the signal and the reinforcer. Response to the CS can be described as "cognitive", since the organisms utilize neutral stimuli to cope with the painful reinforcer in an "objective" way.

Incentive modification, exemplified by gut-defense operates in a completely different manner. For one thing, the toxin can take its effect long after the meal when the organism is asleep, and the palatability of the meal is automatically adjusted commensurate with its utility within the internal economy. If the meal delivers nutritive calories required by homeostasis, that meal will be more palatable next time it is encountered. If the meal produces toxicosis during sleep, that meal will be disgusting the next time, even though the individual cannot remember the illness. Since sleep often follows a meal, this learning without awareness of the UCS is a matter of necessity. A more extensive discussion of the evidence for this phenomenon can be found in Garcia, Hankins and Rusiniak (1974) and in Garcia et al. (in press).

Sensory Hedonics

Affective or hedonic changes are cardinal features of homeostatic conditioning. After eating a tainted meal and becoming ill, a person does not coolly decide that she(he) should avoid that meal in the future because it may cause nausea again. The flavor of the meal now upsets the stomach and inhibits her(his) appetite. In a similar situation, children reject the flavor of ice cream, coyotes retch and hawks smack their beaks in disgust. What was once delicious food is now disgusting. The conditioned response is an emotional response directed at the CS, not a coping strategy directed at a fearful UCS (Garcia et al., 1984). This same hedonic change is characteristic of other homeostatic systems such as temperature regulation. When the core

temperature of a vertebrate organism is cool, a warm stimulus on the skin feels pleasant; when the core is warm the same warm stimulus is unpleasant. Thus, the law of effect directs the organism to a region of optimal temperature. Michel Cabanac (1979) discusses homeostatic regulation in a lucid article with broad psychobiological implications, appropriately entitled, Sensory Pleasure. The Harvey lecture delivered by Curt Richter (1942) on "self-regulatory functions" is a classic in this field.

The best example of this dim sluggish business taking place in the primitive nether regions of the brain is the prolonged delay of poison gradients illustrated in Figure 11 (Palmerino, Rusiniak, & Garcia, 1980). Odor alone can be associated with poison if the toxin takes effect within twenty minutes. On the other hand, taste alone is an effective CS even when the poison is delayed for several hours. When odor and taste are combined into a compound CS, odor is potentiated by taste so that the odor component yields a long delay gradient when tested alone in extinction. Therefore, long-delay learning is not an exclusive function of taste, the long-delay function will be displayed by any sensory system which is shunted into the homeostatic gut-defense system.

These delay gradients were established in rats raised in barren laboratory cages; a recent experiment (Palmerino, Rusiniak, & Garcia, 1980) demonstrated that the slopes are changed dramatically if the rats are given extended experience with a single taste and odor in their cages. Later, when the rats were challenged with a different odor and taste paired with poison, the experienced rats utilized odor cues much more effectively than the naive rats, easily spanning a thirty-minute delay of poison when odor alone was the CS. The odor component of a compound odor-taste CS also served as a much more potent CS for experienced rats. On the other hand, the taste

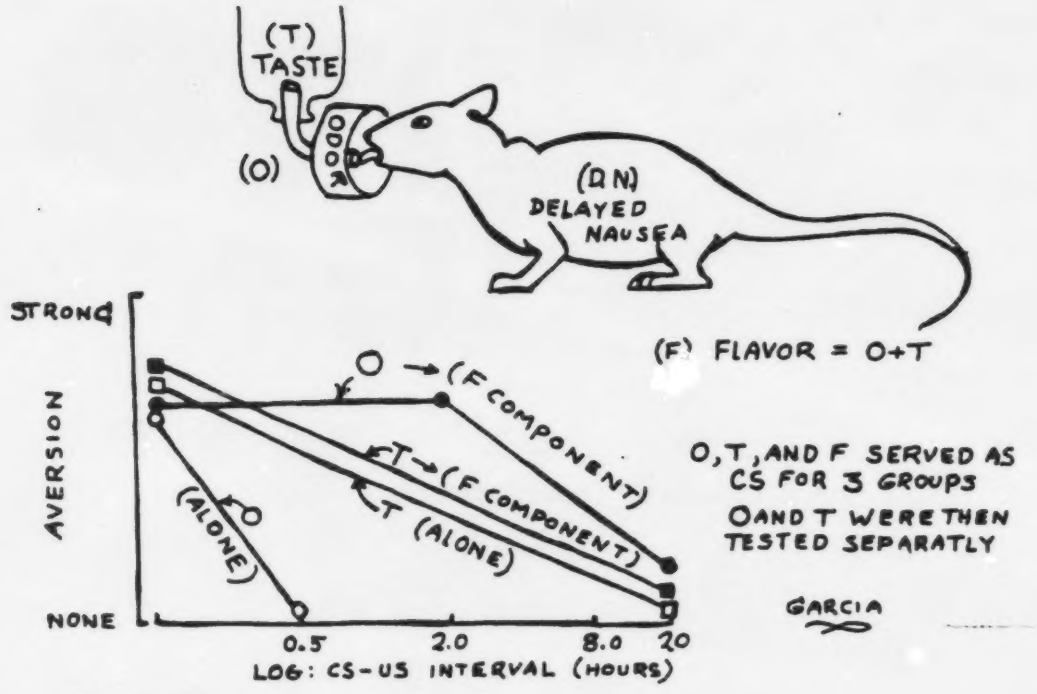

FIGURE 11

POTENTIATION OF ODOR BY TASTE

Figure 11 depicts the span of association for the flavor and the effect of a tainted meal. Emetic injections were given various delays after rats had consumed flavored fluid. When odor was used alone, aversions were absent when the delay of injection was a half hour or longer. When taste was used alone, significant aversions were obtained at two hours and longer. When flavor was followed by varied delays of the emetic US and the odor and taste components were tested alone--the taste gradient was unchanged but the odor gradient was extended. Again taste potentiated odor cues for delayed illness (Palmerino et al., 1980).

gradients were relatively unchanged by the enriched experience with odor and taste. Recall that odor cues are used to search for food in the instrumental phase of the feeding sequence and taste cues are used in the consummatory phase. Thus, these data support Wallace Craig's contention (1917) cited above, that the earlier (odor) components of a behavioral sequence tend to be plastic, while the consummatory (taste) components tend to be more fixed.

SUMMING UP: THE SCIENCE OF LEARNING IN THE CONTEXT OF EVOLUTION

The geological record reveals mainly the hard structural parts of our ancestors, their soft physiological parts are less well-recorded. Behavioral patterns are virtually never recorded and therefore behavior is of little concern to the paleontologist; a habit is not worth a croprolith. This is unfortunate because behavioral patterns in one animal can serve the same ends that anatomical structure and physiological functions serve in another. For example, horses and rodents feed on sandy grass and gritty vegetation wearing their teeth away, but their teeth compensate by continuous growth and repair. Primates do not have such dental specializations, so the babboon must clean the gritty vegetation by hand. Some Japanese macaque have learned to toss sandy rice into the sea to separate the lighter food from the heavier grit. This strategy soon spread by imitation to other members of the troop (see Gould, 1982, p. 299).

We are apt to think that behavioral solutions to survival problems are superior to physiological ones and consequently our near relatives, the monkeys, seem more intelligent than our distant relatives, horses and rodents. This is a self-serving conceit, it is a simple matter to find instances where we use physiological adaptations while our distant relatives use behavioral strategies. For example, we burn up a lot of calories as fuel to maintain a

constant body temperature. We also use behavior strategies, seeking shelter, using fire and lying in the sun. But reptiles are the real experts in behavioral use of solar energy, thus reptiles require about one tenth the food calories that mammals require. Lizards shuttle back and forth between shade and sun to maintain a constant body temperature. As the temperature rises, marine iguanas position themselves parallel to the sun's rays standing with their bodies lifted off the heated rocks of the Galapagos Islands. When they dive into the cold Pacific to feed on seaweed they rapidly dissipate their body heat and lose their mobility, so they come out to flatten themselves on hot rocks raising their body temperature for the next dive. David Attenborough (1979) discusses reptilian temperature control in his book Life on Earth, which summarizes the entire evolutionary history of life in about three hundred remarkable pages of entertaining and thoughtful discussion illustrated with beautiful photographs. A more extended discussion of the topics in this section can be found in ethological textbooks such as Gould (1982), Barnett (1981) and Alcock (1979). There are a number of other excellent volumes, usually with ethology, evolution, and/or animal behavior somewhere in the title.

The Imprinting Option: Innate and Acquired?

The subtle interplay between instinct and learning is best illustrated by what is simplistically called "imprinting". Consider Lorenz and the gray-lag gosling illustrated in Figure 12. Speaking metaphorically, there are two evolutionary options for introducing a newly-hatched gosling to its mother. Nature could have provided the gosling with a hereditary locket containing the portrait of its mother. The gosling would then simply match the mother's features with the mental portrait to discriminate its protective mother from

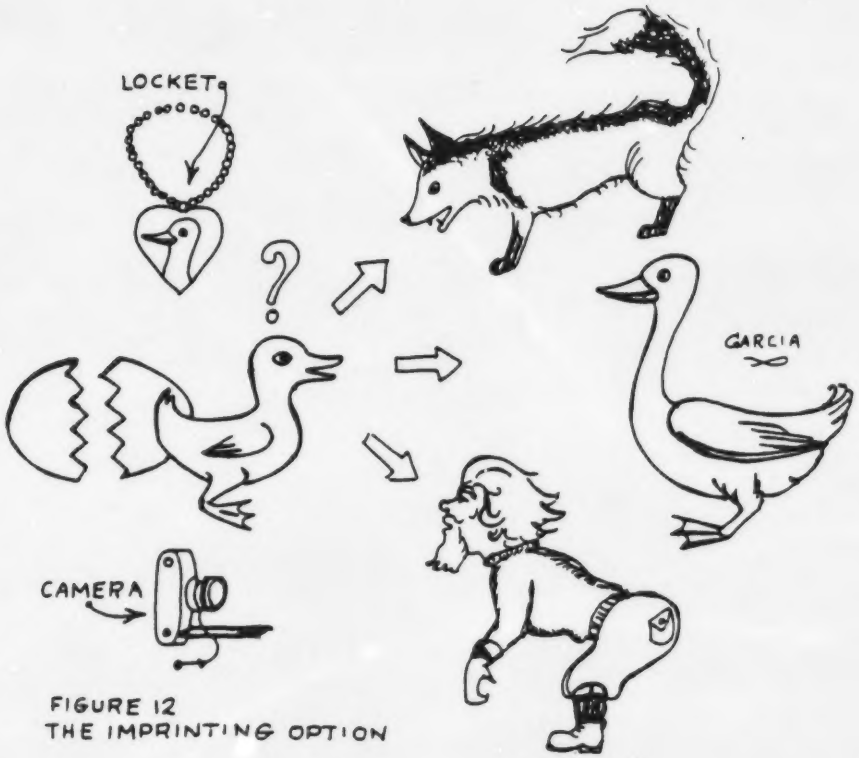

FIGURE 12
THE IMPRINTING OPTION

Figure 12 offers an explanation by analogy for imprinting. Mother nature can insure that the gosling will recognize its mother by giving it a picture of its mother in a hereditary locket. In which case, the gosling would easily discriminate between its mother and the fox, but this information is not of much help since the newborn gosling has no defense against foxes. The mother must be nearby when the gosling hatches if it is to survive. In the latter case, an imprinting mechanism like a camera operates just as well, as Konrad Lorenz demonstrated. A learning mechanism performs the same function as an innate mechanism.

the predatory fox. Alternatively, Nature could have provided the gosling with a learning camera and the following instructions: As you come out of the egg, take a picture of whatever you see moving about; that is your mother, run to her and follow her, she will protect you from the fox. Now, if for some reason, the mother is absent and the fox is present, the gosling with the hereditary locket will run away and the gosling with the learning camera will run towards the fox, but that will make no difference. Neither variant would survive because the predatory fox is incredibly swift and sly.

By squatting on his heels before the hatching goslings and calling like a mother-goose, Konrad Lorenz induced the goslings to follow him as he "duck-walked" through the weeds to the pond. Lorenz's original observations are now criticized because it is difficult to tell which features of his body or behavior was enticing the goslings to follow him. But he demonstrated that whatever the signs were, the goslings became attached to him as the parent. When the goslings developed into mature geese, they were also attached to him as a sex object (see Gould, 1982, pp. 61-65, 267-277). This is reminiscent of Freud's early theory of hysteria: During psychosexual development, a woman is traumatically molested, draining sexual energy in an aberrant way. Later, sexuality is expressed in a hysterical manner related to the intial trauma. In a like manner, Lorenz may have "traumatized" the gray-lag goslings.

The important point is that the gosling is born into a structured evolutionary classroom with the predisposition to learn a great deal about its mother in a brief critical period. The learning mechanisms work as well as hereditary knowledge because the mother must be nearby if the gosling is to survive. Imprinting always appears in a structured context. For example, the white crown-sparrow is also born into an evolutionary classroom. From its

nest it can always hear its father singing the species song in defense of the nesting territory. Later, peering over the nest, it can also watch its father sing. The nestling memorizes its father's song in silence and the following year, it practices the song until it gets it right.

Organisms learn what they must, when they must, in order to survive in the critical period. The mother Herring gull nesting in an open area with flocks of other mother gulls becomes imprinted on the individual features of her own chicks. She will accept any chick as her own for two days after hatching, after that she is likely to kill any strange chick put into her nesting area by an experimenter: The Kittiwake gull nests in the narrow crags and crevasses of rocky cliffs, therefore she does not need to memorize the features of her own offspring since no strange chicks are apt to come wandering in. Thus she will accept any chick which the experimenter puts in her nest (see Gould, 1982, pp. 267-268).

Inherent responses are sometimes directed to very specific features. For example, a red spot on a moving beak is the feature needed to reliably evoke a pecking response of a chick of the herring gull. The mother waves her beak, the chick pecks at the spot, and the mother deliver the food. The chick will peck at a sharpened pencil with some painted bands on its tip as readily as it will peck at a model of its mother's beak (see Gould, 1982, pp. 54-61).

Imprinting is not limited to birds, it occurs probably more often than we know in mammals as well. For example, goats become attached to the smell of their kids when cleaning off the afterbirth tissues. The same thing may happen in sheep for sheep herders often induce a lactating mother, whose lamb has died, to accept an orphan by wrapping the skin of her dead offspring around the strange lamb. Joseph Shepher (1983) presents the case for an

apparent human imprinting phenomena in slim volume documenting his hypothesis with extensive sociological evidence. In the kibbutzim of Israel, unrelated children in the same age range are raised together in nurseries and kindergartens. They live together much like siblings, so when they grow up, they never court or marry one of their own age-group. They form sibling attachments, but not erotic attachments. As children, they explore each others' sexual apparati playing "doctor", but as they approach puberty, they shy away from such intimate contact acting like brothers and sisters. Shepher has examined thousands of individual longitudinal case histories without reporting a single sexual attachment between unrelated adults raised together between the ages of one to six years.

Shepher says that the Kibbutz nursery "fooled mother nature" into believing the unrelated children are siblings. The primitive nuclear family was the evolutionary classroom where children learn that their siblings are not suitable mates. Those variants which did not learn this lesson presumably died out because inbred children do not survive as well as outbred children. Shepher's thesis may be controversial but his evidence is most impressive. Furthermore, the same phenomenon has been observed in other primates. When apes are reared together from birth in a zoo, they also form sibling relationships and it is extremely difficult to induce them to mate according to Warren Thomas, Director of the Los Angeles Zoo (personal communication, 1983).

Convergent Evolutionary Forces

As we pointed out in the beginning, evolution is usually considered a divergent process. Individual members of a species radiate outward, finding differential niches suited to their individual traits. However, there are

convergent forces also. Different species often evolve superficially similar structures adapting tb similar niches. For example, flowers hang at the end of long slender stems in high places offering deep pools with nectar at the bottom to passing animals. In order to harvest the nectar, the animal needs a siphon and the ability to hover in the air flying forward and backward. At least three completely different animals can do this; the nectar-sipping bat is a mammal, the hawk moth is an insect and the humming bird is, or course, a bird. According to evolutionary theory, all three animals diverged from a common ancestor long ago. But more recently in evolutionary time, adaptations have taken place in their differential anatomical mechanisms converging upon the same behavioral niche. Convergent evolution may encourage the belief that pure behavior can be fruitfully studied without attention to anatomical structure. However in that case we would be studying "empty" niches, and as we said in the case of the bar-head goose, a niche cannot be defined independently of the organism which creates it.

Figure 13 illustrates the convergent pressures imposed by the universal "sign-posts" for all long-distance navigators, no matter what species they belong to. While different species may use the same signs, the way in which they do so, is usually unique to that species. For example, the geomagnetic field around the earth provides a reliable directional cue. It is used by humans, birds and bees. Humans use the compass with a magnetized needle which points northward. The needle also points downward as one approaches the north pole because the lines of magnetic force converge down towards the Pole. Humans use the lateral component of magnetic force, but the European robin uses the vertical component. In actual practice, man, bird and bee use geographic features in conjunction with magnetic north to reach their goal.